INTERNATIONAL JOURNAL
OF COMPARATIVE PSYCHOLOGY

NATURALISTIC APPROACHES TO ORANGUTAN INTELLIGENCE AND THE QUESTION OF ENCULTURATION

Anne E. Russon
York University, CANADA

ABSTRACT: Field studies have been, and continue to be, important contributors to the understanding of great ape cognition–especially with regard to questions of cognitive ecology or the key cognitive challenges in the evolution of primate intelligence. They are also critical to resolving a current debate, whether human enculturation boosts great apes' cognition, because only studies of problem-solving in feral contexts can resolve the question of whether abilities are higher in enculturated than non-enculturated great apes. To this debate, this paper offers findings from observational field studies on free-ranging rehabilitant orangutans' cognitive capabilities, as revealed in their food processing and arboreal positioning, and on the possible social transmission of that expertise. These findings are combined with published findings on wild and enculturated great apes as a basis for assessing the effects of human enculturation on great ape cognition. This assessment joins several others in showing that free-ranging great apes independently achieve cognition of the same order of complexity as enculturated great apes, in concluding that claims for the effects of human enculturation are likely inflated, and in suggesting that the basis for the effectiveness of human enculturation is that great apes normally "enculturate" themselves.

INTRODUCTION

Field studies have been important contributors to understanding great ape cognition. My own research, as one example, aims to assess great apes' highest cognitive achievements by studying their solutions to their most intellectually challenging problems. The approach is to isolate these problems on the basis of evolutionary reconstructions which propose selection pressures that could have favored cognitive enhancement in great apes. Modern versions of these pressures likely differ from ancestral ones but may remain near-maximal challenges for living great apes and elicit peak cognitive performances. Whatever

---

Address correspondence to Anne E. Russon, Psychology Dept., Glendon College York Univ., 2275 Bayview Ave., Toronto Ontario, M4N 3M6, Canada. e-mail: arusson@gl.yorku.ca

these pressures are, they concern social or ecological conditions that characterize natural rather than captive environments, that create real problems for great apes, and that engage their problem-solving efforts. This question and this perspective strongly favor studies of spontaneous, species-relevant behavior as it occurs in natural contexts.

It is also important to assess cognition under natural conditions because otherwise, great apes' achievements remain liable to dismissive interpretation as captive artifacts. The current incarnation of this interpretation is human "enculturation", which some claim to bestow higher level abilities on great apes than they attain independently, or create new abilities that otherwise would not exist (Tomasello, Savage-Rumbaugh, & Kruger, 1993; Call & Tomasello, 1996; Tomasello & Call, 1997). Enculturation was originally an anthropological term for immersing an agent in a system of meaningful human relations that includes language, behavior, beliefs, and material culture (Miles, Mitchell, & Harper, 1996). In primate cognition, it refers to rearing nonhuman primates in human settings with the intent of transmitting cultural models and symbolic communication, so that they become active agents within a meaningful system of relations which they come to embody in their own actions and understanding (Miles, 1978; Miles, 1999), or rearing them in human homes where they are treated as agents whose behaviors are intentional (Call & Tomasello, 1996; Tomasello et al., 1993). Enculturation differs from cross-rearing, cross-fostering, or socialization in going beyond simply teaching a static set of rules or skills (Miles, 1978).

My studies of forest-living orangutans in Borneo may shed some light on questions of the impact of human enculturation. These studies concern the cognition governing orangutans' solutions to two foraging problems, obtaining difficult foods and arboreal foraging, because current evolutionary reconstructions suggest they pose the greatest intellectual challenges to great apes (e.g., Byrne, 1997; Parker & Gibson, 1977; Povinelli & Cant, 1995; Russon, 1998). This paper compares my findings on orangutans' cognitive achievements with similar findings on wild and enculturated great apes, and assesses the potential for cultural transmission in these orangutans' achievements.

Findings on orangutans represent data collected from 1995 to 1997 on ex-captives reintroduced to a protected forest, Sungai Wain, by the Wanariset Orangutan Reintroduction Project (ORP) (Figure 1). A total of 82 orangutans were reintroduced into this forest from 1992 to 1996, in six groups and at five different sites (K1-K5 on Figure 1). At their release they varied in age from older infants to adults, with most in the young juvenile to young adolescent range. I observed 18 orangutans who ranged near two release/provisioning sites, K3 and K5; all were

between 4-15 yrs of age and 0-6 yrs' experience in Sungai Wain. I observed two of them over three years, five over two years, and eleven in one year. Nine of them were members of a large group reintroduced to the forest in 1996; all were monitored for their first two months post release and four were followed a year later. Sungai Wain Forest lies just outside the city of Balikpapan, East Kalimantan, Indonesia. Officially, it comprises 9,783 ha of lowland mixed dipterocarp forest with extensive swamp areas but encroachment, drought, and fire have reduced it to about 3,500 ha (Russon & Susilo, 1999). Data collection was structured as event sampling (target events were bouts of obtaining a key food item) within a framework of full-day focal individual follows. Observations totalled +/- 400 hrs in each year.
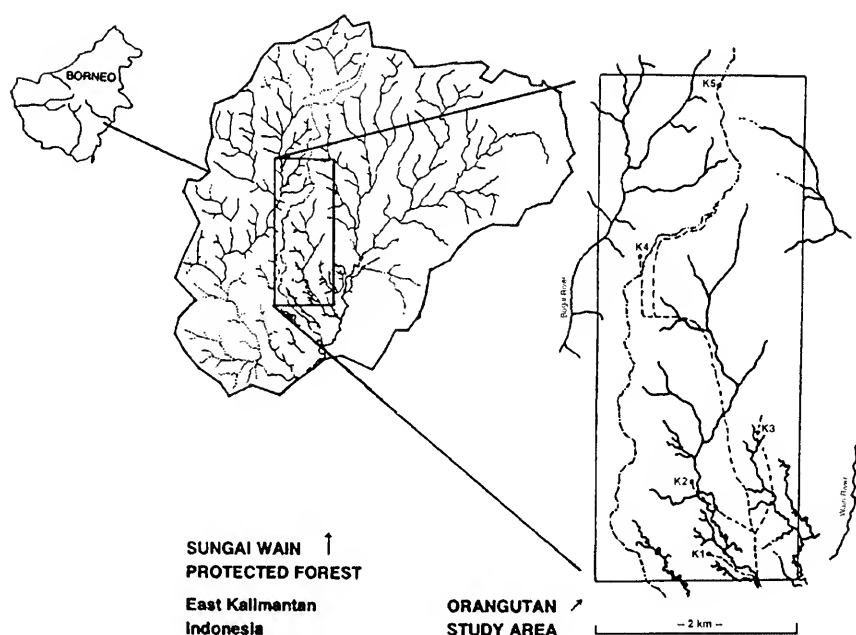
Figure 1. Sungai Wain Forest, E. Kalimantan, Indonesia.

Measuring Cognition

Assessments of the cognition governing great apes' performances are open to interpretation and considerable dispute. This results, in part, from complexities in the body of available data. Empirical studies have adopted a variety of cognitive models, measures, and tasks, and this variation is substantial between free-ranging and captive conditions. In addition, much of the relevant data on free-ranging great apes was collected for other purposes and was neither described nor analyzed with cognition in mind. Despite the difficulties this creates for an integrated interpretation of great ape cognition, and for comparing enculturated with free-ranging great apes, two major reviews of great ape cognition have recently appeared (Parker & McKinney, 1999; Tomasello & Call, 1997). I have relied primarily on these reviews for comparative discussions because they offer up-to-date, integrative overviews. Tomasello and Call lean to skeptical interpretations and Parker and McKinney to generous ones, so the two positions can be taken as bracketing the range of interpretations currently considered plausible.

Both reviews faced the difficulty of finding theoretical models that afford integrating a highly diverse body of information. As a basis for understanding their interpretations I have sketched their positions on physical world cognition, which refers to the suite of abilities used to handle problems in the physical as opposed to the social world (e.g., space, logic, cause-effect, quantity). These are the cognitive abilities most relevant to foraging and arboreal problems. Both favor models of cognition as products of evolution and ontogeny, where environmental pressures and experience are important contributors to the cognitive capabilities realized, and both rely heavily on Piagetian-based models and measures of cognitive complexity.

Tomasello and Call focus on sensorimotor or first-order cognition modeled as an ordered series of stages spanning human cognitive achievements from birth to 18-24 months of age. Primarily, these achievements involve the construction of cognitions or "schemata" for ordering simple sensory and motor phenomena (Piaget, 1952; Piaget, 1954; Piaget, 1962). First-order cognition spans the range of cognitive processes traditionally considered applicable to nonhuman species, such as reflex-driven action and schemata for simple motor actions, objects, forces, or object sets. It culminates, in stage 6, with the achievement of rudimentary symbols. In physical cognition, early symbols commonly represent object-object relationships like "in" or "on" and show primitive understanding of abstract relational categories.

Parker and McKinney (1999) also consider first-order cognition but extend their consideration to capabilities that emerge in human development beyond the sensori-motor period. The move beyond first-order cognition is seen as the product of cognitive hierarchization or metarepresentation, i.e. building new cognitions by re-representing existing ones. The first form of hierarchical cognition that emerges is often termed second-order cognition; like first-order cognition, second-order cognition spans several levels of complexity (e.g., Langer, 1996; Whiten & Byrne, 1991). Case (1985) offers one of the few methods for indexing rudimentary hierarchical cognition, based on his model of second-order cognition as "interrelational", that is, second-order cognition processes phenomena in terms of the simple physical relationships (object-object relationships) involved and the cognitive structures that coordinate several physical relationships with one another (interrelational structures). The number of object-object relationships that can be handled in a coordinated fashion, within one overarching interrelational structure, can be used as an index of the level of second-order cognition being used–the more relationships coordinated within one structure, the higher the level (Case, 1985; Parker & McKinney, 1999; Russon & Galdikas, 1993).

Cognition in food processing

Food processing refers to preparing food items for consumption. It is considered to pose challenging intellectual problems for great apes because some of their essential foods are "technically" difficult, i.e., embedded and/or otherwise defended from predation (e.g., Byrne, 1997; Parker & Gibson, 1977). Among the more difficult foods in Sungai Wain are two permanent foods, colonial nest-building termites and the meristem (heart or cabbage) of several palm species. The most difficult of the termites consumed are embedded, within their nests; some of the nests are cement-hard, invisibly buried underground, and tangled within a maze of tree roots. The palm's heart is also embedded, either within a crown or beneath a tough sheath; it may also be protected by additional physical defenses, such as fences of sharp spines or razor-edged leaves and petioles, or by chemical defenses, such as bitter flavors or otherwise noxious chemicals (Jones, 1995). Palm heart also represents a set of naturally graded problems rather than a single problem because palms range in size from slender immature rosettes on the forest floor to massive crowned trees 10-15 m tall.

Any one such food may then present several difficulties, so processing these food commonly requires elaborate processing strategies involving the coordinated use of several different kinds of

food manipulation.   The strategy for removing bark has several variants, for instance, including biting off small bits repeatedly to make a long trench along the underside of a branch or scoring the bark by biting it repeatedly along a length then tearing off the whole loosened strip in one pull.   Analyses of the orangutans' complex strategies for obtaining heart material from *Borassodendron borneensis* palms indicated hierarchical cognition (Russon, 1998).

This finding on food processing in orangutans complements findings on wild great apes. Hierarchical cognition has been detected in the food processing techniques of mountain gorillas (e.g., Byrne & Byrne, 1991) and chimpanzees (e.g., Matsuzawa, 1991, 1994; Yamakoshi & Sugiyama, 1995).   In chimpanzees, some of these hierarchically governed food processing techniques are tool-assisted. Using Case's model of second-order cognition, several tool-based techniques used by chimpanzees involve coordinating two object-object relationships (one interrelational structure), e.g., probing for ants/termites (probe-nest, probe-ants/termites) and cracking nuts with hammer-and-anvil tool sets (hammer-nut, nut-anvil).   This level is typically achieved by 27-40 months in human children (Case, 1985).

One of the most complex food processing techniques known in wild great apes involves a tool set with a "metatool", i.e. a tool that is used to make another tool. Matsuzawa observed three chimpanzees at Bossou who cracked nuts with hammer-anvil tool sets adding a third rock as a wedge to level their anvil rock, i.e., to modify or improve their anvil tool.   Assessing Bossou chimpanzees' metatool use for its cognitive complexity is important: In addition to being one of the most complex forms of spontaneous food processing in great apes, both reviews consider this case and metatool use is one of few phenomena that can be compared directly across enculturated and free-living apes. Parker and McKinney's interpretation concurs with two others (Matsuzawa, 1996; Russon & Galdikas, 1993) that this metatool use coordinates three object-object relationships in one interrelational structure (wedge-anvil, anvil-nut, hammer-nut).   This level of complexity is not typically achieved by human children before 40-60 months of age (Case, 1985). Tomasello and Call review this metatool use but offer no analysis beyond their overall assessment that, at best, some great ape tool use may show stage 6 first-order cognition. They offer this assessment with caution, however, on the grounds that the nature of background experience (with its implied trial-and-error learning) is not precisely known.

The tasks presented to enculturated great apes that most resemble food processing in their cognitive demands are using tools and manipulating objects, which invoke causal abilities mainly (means-end

or cause-effect reasoning, especially in force-based manipulation) and logical abilities sometimes (if alternative techniques or tactics are used). Several captive great apes, some of whom were enculturated, have mastered metatool use. Two captive chimpanzees learned to use a rock to break open a bone for food inside, then used a fragment of the bone to pierce a skin covering a desirable drink (Kitahara-Frisch, Norikoshi, & Hara, 1987), and an enculturated language-trained bonobo (Kanzi) and a captive orangutan learned to make flake tools from humans, then used them to cut ropes for access to food (Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993; Wright, 1972). Parker and McKinney credit human enculturated great apes with achieving second-order cognition in their solutions to such tasks. Tomasello and Call hesitate to credit their metatool use fully because all cases reported were heavily scaffolded by humans; their assessment of enculturated great apes' tool use and causal abilities remains stage 6 first-order cognition at best.

Based on difficult food problems, wild and other free-ranging great apes attain cognitive levels similar to those attained by enculturated great apes: second-order cognition. Free-ranging chimpanzees independently master metatool use, the most cognitively sophisticated product, while enculturated great apes have mastered it only with extensive human scaffolding. This contradicts the effects claimed for human enculturation because it is free-ranging great apes, not human enculturated ones, that demonstrate, independently, the highest level cognition.

Cognition in arboreal life

Arboreal life, in the form of arboreal travel, has been considered to pose critical cognitive challenges for great apes (Bard, 1993; Chevalier-Skolnikoff, Galdikas, & Skolnikoff, 1982; Povinelli & Cant, 1995). Among the challenges identified are long-distance navigation through dense tropical rain forest, establishing travel routes through the discontinuous forest canopy, and moving their exceptionally large and heavy bodies through a canopy that does not readily support such weight. Food more than travel, however, is considered the main reason that primates are in the trees and the major influence on their locomotor habits (Fleagle, 1984). Arboreality adds several complications to the problem of obtaining difficult foods, notably arboreal positioning for *accessing* food and arboreal positioning for *manipulating* food, and each can be cognitively challenging (Cant, 1987; Povinelli & Cant, 1995; Russon, 1998).

Analyses of juvenile rehabilitant orangutans' arboreal locomotion during their approach to arboreal food sources indicated hierarchical cognition (Russon, 1998). One juvenile rehabilitant male made a proto-tool, a handle for his vehicle tree. Vehicle trees, themselves proto-tools, are slender pole trees that orangutans sway deliberately to cross the gap between their current position and their next target tree (Bard, 1993). This juvenile male made his handle by cracking a branch of his vehicle tree until it dangled loosely; holding the handle, he could reach farther than he could by holding his unmodified vehicle tree and successfully transferred into his target food tree (Russon, 1998). This handle comes close to a metatool because, like Matsuzawa's wedge, it modified a tool--the vehicle tree proto-tool. Limited observations in 1998-99 suggest that adolescents and adults, perhaps because they are heavier-bodied than juveniles, may construct more elaborate proto-tools to position themselves for obtaining arboreal food items. One adolescent male positioned himself on two slender pole trees near an arboreal food item, then climbed the two trees like a rungless ladder to access the food. Spatially, this involves coordinating at least two object-object spatial relationships, disregarding the self: pole trees–food, pole tree–pole tree. One adult female also used two pole trees to access a food item and in addition modified them to make a seat on which to sit while processing the food. She chose two slender pole trees, spaced $\pm$ 1.5 m apart and within reach of a rattan food, then climbed into them. She pulled the two trees across one another to form an "X" then sat in the side of the X closest to the rattan, her weight on its lower leg and one arm holding the adjacent upper leg for balance. To position herself arboreally for obtaining the rattan, she coordinated at least three object-object relationships: pole tree--pole tree (initial, spatial), pole-tree–pole-tree (modified, causal), pole-trees–rattan (spatial).

Some earlier studies of the cognition governing free-ranging orangutans' arboreal navigation and locomotion have detected upper-level first-order cognition (Bard, 1993; Chevalier-Skolnikoff et al., 1982). These studies did not assess cognition beyond the first-order level, however, and Bard's study focused on cognitively immature youngsters, but both hint at cognition that is more complex. Both describe use of vehicle tree "proto-tools". To the extent that the "self" figures into calculations as an object of a particular size and weight to be manoeuvered through the canopy (Povinelli & Cant, 1995), vehicle tree use suggests coordinating two object-object relationships (self-vehicle tree, vehicle-tree–target tree). Povinelli and Cant's own descriptions of orangutans' clambering mode of arboreal locomotion suggest hierarchical cognition. These findings likewise point to great

apes' attaining hierarchical cognition in their arboreal positioning; that is, at least second-order cognition.

Tasks for captive great apes that most resemble the complex arboreal problems of feral life are spatial and causal tasks. Spatial tasks are relevant because arboreal positioning and travel entail identifying relationships between forest structures (and the self) that afford travel trajectories and/or provide bodily support. Causal tasks are relevant because orangutans deliberately apply force to deform vegetation during arboreal travel or positioning. Using force to change the physical world is a classic application of causal reasoning (Chevalier-Skolnikoff et al., 1982). Tomasello and Call review studies on great apes' spatial cognition based on complex maze or obstacle/ detour tasks, but this research is patchy and does not single out enculturated apes. The findings they consider include several chimpanzees tested on both types of tasks but only single members of the other great ape species, tested on one of the tasks. Tomasello and Call find no evidence for spatial cognition beyond sensorimotor stage 6 in any captive great apes. Parker and McKinney include additional studies on spatial cognition which show stage 6 first-order cognition in great apes as young as 4 years old (e.g., Poti', 1996) and second-order cognition in older great apes, to levels seen in 3-year-old human children. Great apes' highest levels of spatial cognition have been shown in drawing tasks; one top performer was Chantek, a human-enculturated orangutan (Miles et al., 1996) but the second was a zoo chimpanzee unlikely to qualify as human enculturated (Morris, 1962). Parker and McKinney conclude that great apes achieve second-order cognition spontaneously in solving spatial problems and that enculturated great apes may reach slightly higher levels but these remain within the second-order range. Their conclusion is based on evidence from a range of spatial tasks, including block assembly, drawing, symbol reading, and knot tying.

Here too, the cognitive achievements of free-ranging great apes are on a par with human-enculturated great apes and may even exceed them, if Tomasello and Call's interpretation is accepted.

Centralized Cognitive Mechanisms

An alternative to assessing cognition in terms of abilities is to consider centralized generative mechanisms. Three centralized mechanisms are considered to underlie human cognitive achievements-- combinatorial mechanisms, hierarchization, and integration (e.g., Langer, 1996). Hierarchization has been discussed. Combinatorial mechanisms create combinations of multiple mental items, to allow handling them simultaneously. They often operate in conjunction with

hierarchization in humans, as "hierarchical mental construction", so that higher-level cognitions comprise several lower-level cognitions coordinated into a new higher-level one (e.g., Gibson, 1993). Integration affords interconnections or interplay between different types of cognition, i.e. relatively independent sets of special-purpose cognitive structures like causal or logical abilities, to allow applying several to a single problem. Many problems are solved best, or only, by several abilities used interactively rather than one ability used alone. Integration is considered the most sophisticated of the three processes because it can operate only within cognitive systems that are already hierarchical (Langer, 1996). Hierarchization and combinatorial mechanisms are relatively well studied in nonhuman primates, the former because of its apparent role in great ape cognition and the latter because it is considered common. Integration has received less attention, partly because studies have focused on problem-specific cognitive abilities and partly because integration has been considered beyond nonhuman primates' capacity (e.g., Langer, 1996).

Rehabilitant orangutans' handling of arboreally-located difficult foods suggests cognitive integration, which may therefore have considerable significance for models of great ape cognition. Arboreal location increases difficulties in obtaining difficult foods because it adds a second complex task that must be handled simultaneously. Increases in difficulty go beyond adding more tasks, moreover, because food processing and arboreal positioning entail different cognitive abilities (food-causal; positioning-spatial) and the two tasks can interact (e.g., orangutans shift their arboreal position to accommodate food processing activities). Orangutans are also not physically equipped to handle the two tasks independently: they have in total five manipulators but each task often requires three. Orangutans' arboreal feeding postures enlist three manipulators over 60% of the time (Cant, 1987; Reynolds, 1991; Kaplan & Rogers, 1994). Some of their food processing operations also involve three manipulators; two hands may be used to tear apart a tough protective matrix, for instance, while a third hand or the mouth pulls the desired inner item out (Russon, pers. obs.). When a difficult food operation coincides with a difficult feeding posture, the two tasks can simultaneously require three manipulators (Russon, 1998).

Orangutans cope successfully with arboreally-located difficult foods and they do so by interconnecting their solutions to the two problems. Examples of tactics include sharing a manipulator between the two tasks (using a manipulator to contribute to positioning and food processing simultaneously) and briefly transferring a manipulator from one task to the other (e.g., a hand may drop its positioning role to assist

with food processing, then return to its positioning role a few seconds later). Both tasks can require second-order cognition, so the combined problem itself could in some instances entail integrated use of second-order causal and second-order spatial cognition. In proto-tool-assisted arboreal positioning, these orangutans also showed integrated use of two types of cognition--spatial abilities to identify an appropriate initial spatial layout and to envisage an improved one, and causal abilities to modify the support or vehicle trees. Interconnected solutions point to cognitive integration–that is, orangutans can and do apply multiple abilities interactively.

Wild great apes also offer evidence cognitive integration, in the form of applying multiple cognitive abilities to one problem. Examples include chimpanzees substituting tools, because identifying equivalent tools involves applying logical abilities to a causal problem (Sakura & Matsuzawa, 1991), and orangutans using spatial abilities to establish initial and equivalent spatial layouts for obtaining food with tools (Fox et al., 1999).

In captive great apes, interactions between cognitive abilities that have been detected include: language abilities enhancing logical abilities (language-trained chimpanzees performed at higher levels on analogy problems than non-language trained chimpanzees--Premack, 1984), logical and causal abilities combining to expand the basis for classification and the range of means-end behavior (e.g. classifying items by their causal function or identifying equivalent items that can function as the same tool--Langer, 1996; Russon, 1996a), and imitation contributing to causal understanding (e.g., imitation contributing to the acquisition of tool use--Meinel, 1995; Toth et al., 1993). Some of the performances suggesting cognitive integration were by human-enculturated great apes, but others were not.

Both free-ranging and enculturated great apes offer evidence of cognitive integration. If anything, the expression of cognitive integration may be more robust in free-ranging great apes because it is needed to handle problems that are encountered on a daily basis. Its expression by enculturated great apes is liable to dismissal as scaffolded, whereas it is not in free-ranging great apes. If anything, the ensemble of findings suggests that free-ranging great apes express these most complex generative processes more strongly than enculturated great apes.

Contributions of social transmission

Enculturation entails, at minimum, social transmission of some facets of these cognitive capabilities. In the rehabilitant orangutans,

several lines of evidence point to social transmission as an important contributor to their foraging expertise.

Bandang hearts.   The heart (meristem) of *Borassodendron borneensis* palms (locally, *bandang*) is a preferred food among Sungai Wain orangutans as well as a key permanent one. The palm's heart is embedded within its stem near its growing tip. In *bandang* seedlings, it is in the center of a small, slender-leafed rosette on the forest floor. In mature *bandang*, it is atop a sturdy trunk rising 10-15 m tall, embedded within a massive fibrous crown, and surrounded by 50-100 sturdy, sharp-edged leaf stalks.   These orangutans' technique for obtaining *bandang* hearts is to pull the newest leaf out of its socket then bite the heart matter from the base of the pulled leaf. Tactically, the set of manipulations applied varies with the size of the palm.

Nine of the 18 orangutans I followed were naive to *bandang* heart when I first observed them. Only 3/9 acquired techniques for obtaining *bandang* hearts within my three years' observations—Paul, Enggong, and Bento, juvenile males 5-6 yrs old who had ranged near site K3 for 0.5, 1.5, and 2 yrs respectively. In my first month I followed each for three days (85 hrs total) and observed none eat *bandang* heart although all often ate a simple *bandang* food, the leaf blade. Sariyem, a juvenile female +/- 5 yrs old, twice visited the K3 area for 3-4 days in the following 1.5 months and while there she obtained and ate several *bandang* hearts. The males all scrounged *bandang* heart from her and one once pulled a new leaf from a small *bandang* but then ate its tip. Between Sariyem's visits, none of the males was observed eating *bandang* heart (55 hrs/8 days observation) but six months later, all three regularly obtained *bandang* hearts independently. This suggests that their expertise with *bandang* hearts started with input from Sariyem. They could have acquired the expertise independently but this seems unlikely because they had not done so despite ample opportunity (.5 to 2 years' living in areas where this food was abundant) and all three males acquired the expertise over the same short period despite large differences in forest experience.

Six other orangutans appeared naive to the technique for *bandang* hearts at their release in Sungai Wain at site K5. Four of the six were followed one year later and two of those four were followed a year beyond that, all still apparently naive. The six naive orangutans were from a group of 22 that I followed over the first two months after their release in 05/96. During those observations (110 hrs/18 days), 3/22 orangutans independently obtained *bandang* heart but all three left the area rapidly (one within two days and second within a month; the third stayed three months but she was a very young juvenile with only rudimentary expertise). Naive orangutans' failure to acquire *bandang*

expertise coincides with their lack of social learning opportunities.

Rattan hearts. Orangutans obtained rattan hearts using a technique similar to that for *bandang* hearts; the tasks are similar since rattans are climbing palms (Jones, 1995). Rattan hearts are simple to obtain from immature plants at the sucker stage. Rattan suckers are much like *bandang* seedlings, small rosettes on the forest floor with new leaves like slender shoots of grass that can be extracted in one easy pull. Nonetheless, some newly released orangutans did not obtain rattan shoots or recognize them as food. One, Jaja, did not acquire this expertise even though other orangutans pulled and ate shoots before her eyes. Our observations and background information from the reintroduction project suggest that the likely reason was that Jaja was highly human-oriented and did not interact with orangutans. A young woman student whom Jaja liked finally taught Jaja how to obtain rattan shoots by demonstration. In front of Jaja, she pulled out a rattan shoot, pulled it apart a little at the bottom, then ate its tender base. Jaja watched then took a rattan leaf and pulled it apart, but ate the tip instead of the base. The student demonstrated the correct technique again and gave Jaja the shoot. Jaja ate it immediately, pulled one on her own, then spent the rest of the day going from rattan to rattan, pulling then eating their shoots.

Bandang Pith. From *bandang*, these orangutans also often ate pith from the leaf petiole. Processing entails tearing the petiole open lengthwise, pulling strips of fibrous pith (parenchyma) away from the sheath, and chewing the strips for their juice.

In the first month after their release at K5, none of three small females (Kiki, Ida, Siti, +/- 5 yrs old) was observed eating *bandang* pith although they were monitored by researchers and project technicians daily. Technicians observed and recorded Kiki's independent discovery of this food and her inventing a technique for obtaining it. Ida and Siti, who commonly traveled and foraged with her, immediately began scrounging Kiki's *bandang* pith. Within two weeks Sit was obtaining this pith independently.

Petiole choice for *bandang* pith suggested social influence. In 1995 and 1996, all three males ranging near K3 ate *bandang* pith from mature leaves but never from the newest or second newest leaf. In 1997, only two females ranging near K5 ate *bandang* pith, Judi and Siti, who had become regular traveling companions since their release in 1996. Both ate pith from the second newest leaf but never either mature or newest leaves. Competition played no role in selection. No others near K5 ate this pith, *bandang* palms are plentiful, and each palm has 50-100 mature leaves to one second newest leaf.

Social influences were also likely in Judi and Siti's techniques for

obtaining *bandang* pith. These two often selected palms with a liana or branch running horizontally or diagonally through the crown. To expose pith, they regularly made their first bite into the petiole sheath near the leaf base. This often cracked the petiole and it often flopped over the liana/branch. The liana/branch then served as a hanger for the petiole, probably helping secure it in place as they tore it apart. I did not detect this pattern until late in my data collection so I lack reliable figures on its frequency of occurrence. It occurred on at least five occasions, however, which suggests that the layout and place of biting were deliberate parts of their processing technique. No other orangutans were observed using this tactic. Orangutans near K3, in contrast, normally made their first bite about a third of the distance down from the leaf base and never used a hanger.

Daun Biru Pith. Orangutans ate pith of another palm common in Sungai Wain, *Licuala sp.* (locally, *daun biru*) but only, to our knowledge, after 1997-98 drought and fires (Fredriksson, 1995; Peters, 1995; Russon, unpub. data). In 06/97, directly after the drought and fires, I followed Tuti, an adolescent female released at K2 in 1993. Within half a day, she ate pith from several *daun biru* palms, tearing open 5-6 petioles from each palm. After Tuti had finished a palm, its crown was badly shredded and broken. Neither project staff nor researchers had reported seeing *daun biru* palms in this state of destruction in the four years prior to the drought and fires. Staff and researchers followed and observed the rehabilitants regularly and this damage was very striking, so observers would not have missed this damage if it had been common. I concluded that this was a new food and a new technique that Tuti acquired after the drought and fires. Within a month I followed Charlie, a subadult male released at K1 in 1992. Within a day he ate *daun biru* pith and left the palm in a similar state of destruction. Charlie and Tuti were known to travel together, intermittently, for several days at a time. It is likely that they were pushed to find new foods because of scarcities occasioned by fires and drought; either one of them discovered this food and the technique independently then transmitted the expertise to the other while travelling together, or they developed the expertise jointly.

Bark. Aming, an adolescent male with four years' experience in Sungai Wain, was translocated to K3 in 1996. On his first day there, he ate bark from a tree that bore no signs of previous bark removal even though it was located within 20-30 m of K3, at the intersection of two main trails that the residents had used daily for at least 1.5 years. Enggong approached and watched the work intently over Aming's shoulder. Enggong neither scrounged Aming's bark nor began eating bark independently elsewhere in the same tree--either of which would

have been the normal if he had been familiar with this food. As soon as Aming left, Enggong took the position Aming had just vacated and tried to remove bark from the place that Aming had been working. Enggong used the same basic technique as Aming, biting then tearing bark off, but he succeeded in freeing only tiny chips of bark per bite whereas Aming could free long lengths. These observations suggest that this particular bark food was unknown to Enggong before observing Aming, and that Enggong learned its identity and something of its processing technique by observing Aming.

Avenues and mechanisms of social learning. These incidents illustrate at least three types of social experience in these orangutans that could contribute to social transmission of food-related expertise: scrounging, scavenging, and coaction. Social learning mechanisms that could operate during coaction (a learner's intimate participation in an expert's activity--Visalberghi & Fragaszy, 1989) include stimulus and response priming, social reinforcement, shaping, and imitative (observational) learning. Those afforded by scavenging and scrounging include local or stimulus enhancement induced by the producer's behavior or its aftereffects and imitative learning. All these mechanisms are within great apes' cognitive reach. That social transmission supports orangutans' acquisition of complex expertise is then entirely plausible.

IMPLICATIONS

These findings have implications for the problems and models appropriate for assessing great apes' cognitive capacities, the cognitive achievements of free-ranging versus enculturated great apes, and the impact of human enculturation on great ape cognition.

Orangutans' difficult foods often pose multiple problems, in the form of a diverse host of anti-predator defenses. When these foods are arboreally located, as they often are, the problems multiply in number, diversity, and interactive complexity. This contrasts with the unidimensional (single ability) problems aimed at sensorimotor level cognition that have commonly been posed to captive great apes (Russon & Bard, 1996). The implication is that forest problems tap more complex cognitive processes.

A prerequisite for assessing great apes' cognitive achievements is resolving discrepancies between the interpretations offered by Parker and McKinney versus Tomasello and Call. They agree that relational understanding is a key feature of great ape cognition, in the sense of understanding how external entities or third parties relate to one another

when the actor is not directly involved. Their major difference concerns whether relational understanding represents the ceiling or the threshold of great apes' highest cognitive capacities. Tomasello and Call offer a ceiling-like interpretation, because they offer a flattened view of relational cognition as representing a narrow range of understanding--understanding relational categories. While first-order cognition culminates in the understanding of abstract relational categories, beyond its scope is the interrelational understanding required to manage interplay among multiple relational categories. Interrelational understanding underpins a significant range of capabilities, perhaps the whole of the pre-operational or second-order stage that characterizes human cognition between about 2 and 6 years of age (Case, 1985). This suggests problems with Tomasello and Call's preferred models, which span only first-order cognition systematically. First-order models lack the conceptual and methodological tools to index some of great apes' complex techniques, including metatool use, because these techniques require coordinating interplay among multiple relational categories. When models of second-order, interrelational cognition are used to analyze great apes' techniques, as they are by Parker and McKinney and by others (e.g., Byrne & Byrne, 1991; Byrne, 1995; Langer, 1996; Russon, 1998; Russon et al., 1998), evidence of interrelational cognition is clear up to levels found in human 3-year-olds.

In this light, free-living orangutans as well as gorillas and chimpanzees show cognitive levels on a par with enculturated great apes. In addition, their solutions to feral problems tend to be "orchestral" in the sense that they involve using multiple cognitive abilities (e.g., Parker & McKinney, 1999). It is in orchestral problem-solving that great apes offer evidence of cognitive integration, in the form of interconnected use of social, logical, causal, and spatial abilities. In free-ranging great apes this sort of cognitive interplay occurs frequently; in enculturated great apes, it has rarely been detected. Enculturated apes' achievements are also human scaffolded while free-living great apes' are not. The appropriate conclusion is that free-ranging great apes achieve equally if not more advanced capabilities than enculturated great apes in physical world cognition.

These findings also reflect on models of great ape cognition. They indicate that great ape cognition is better construed as a system of interconnected abilities designed for handling multifaceted problems than as an aggregate of independent, module-like abilities for handling unidimensional ones. Most studies of great apes have adopted traditional models that portray nonhuman cognition as an aggregate of isolated ability structures (e.g., Cheney & Seyfarth, 1990; Davey, 1989; Hirschfield & Gelman, 1994). Few have advocated interconnectedness

between semi-independent abilities (e.g., Mitchell, 1994; Parker, 1996; Rumbaugh & Pate, 1984a, b; Whiten, 1996; Whiten & Byrne, 1991; and Tomasello & Call, 1997, promote this for all primates). Findings on reintroduced orangutans support interconnectedness as the more appropriate model. Findings also suggest that studies designed around module-like abilities likely underestimate great apes' full intellectual power.

These findings do not imply that enculturation, in the sense of the cultural transmission of expertise, plays no important role in great apes' cognitive capabilities. Sungai Wain orangutans appear to make substantial use of social transmission in acquiring foraging expertise, as do wild chimpanzees, gorillas, and orangutans (e.g., Boesch, 1993; Byrne & Byrne, 1993; Fox et al., 1999). Free-ranging great apes show sophisticated social learning mechanisms that could support cultural transmission, such as imitative learning (e.g., Russon & Galdikas, 1995; Russon, 1999) and demonstration teaching (Boesch, 1991, 1993). It is now widely accepted that expertise is culturally transmitted in chimpanzees (e.g., McGrew, 1992; Whiten et al., 1999; Wrangham, McGrew, de Waal, & Heltne, 1994) and orangutans are suggesting similar patterns (Fox et al., 1999).

While this makes it likely that human enculturation has an important effect on great ape cognition, findings suggest three caveats. (1) It is likely that human enculturation can enhance great apes' cognitive capabilities because cultural forces are normal facets of great ape cognitive development in the wild–as Parker and McKinney put it, wild great apes "enculturate" themselves. (2) Human enculturation probably bends great apes' cognition in atypical directions because great ape cognitive development is dependent on experience, as it is in humans. A great ape's cognitive capabilities should take on the shape of his or her individual rearing conditions and living problems, as is evident in human-enculturated great apes' developing abilities that are not apparent in feral conspecifics, like mathematics or language. By the same token, however, enculturated great apes show impoverished cognitive capabilities when faced with forest problems like processing foods or navigating. Among ex-captive orangutans newly reintroduced to forest life, human-enculturated ones stand out painfully for their poor cognitive capabilities. Even after having experienced forest foods, climbing apparatus, and orangutans during rehabilitation, once in the forest they have difficulty recognizing even common forest foods, ignore cues to forest living from other orangutans, and are inept at figuring out how to obtain foods, travel arboreally, and navigate through the forest (Russon, 1996b). What human enculturation seems to offer, then, is refinement of problem-specific abilities that are

important in human contexts. (3) The impact of human enculturation has likely been exaggerated. Parker and McKinney offer what may be the best analysis of the forces involved, based on work by Fischer et al. (1993). Fischer and co-workers have shown that an individual's cognitive competence with a given type of problem constitutes a range of levels, not a fixed level, and that unsupportive contexts elicit low levels in the range while socially supportive contexts elicit high levels (Fischer et al., 1993). The exceptional performances of human-enculturated great apes have occurred in socially supportive conditions, so they could represent the highest levels of these apes' current competence range which were expressed because of especially supportive conditions.

Naturalistic field studies have been important recent contributors to the understanding of great ape cognition and they will remain essential when addressing questions concerning cognitive ecology, cognitive evolution, and the like. It is such studies that have convinced scholars that great apes have cultures (e.g., Boesch, 1996; McGrew, 1992; Whiten et al., 1999; Wrangham et al., 1994) and it is only such studies that can provide the evidence needed to resolve the issue of the impact of human enculturation on great ape cognition. It appears that reports of the impact of human enculturation have been greatly exaggerated.

ACKNOWLEDGEMENTS

REFERENCES

Bard, K. A. (1993). Cognitive competence underlying tool use in free-ranging orang-utans. In A. Berthelet & J. Chavaillon (Eds.), *The Use of Tools by Human and Non-Human Primates* (pp. 103-113). Oxford: Oxford University Press.
Boesch, C. (1991). Teaching among wild chimpanzees. *Human Evolution, 6,* 81-90.
Boesch, C. (1993). Aspects of transmission of tool use in wild chimpanzees. In K. R. Gibson & T. Ingold (Eds.), *Tools, Language, and Cognition in Human Evolution* (pp. 171-183). Cambridge, UK: Cambridge University Press.
Boesch, C. (1996). Three approaches for understanding chimpanzee culture. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into Thought: The Minds of*

the Great Apes (pp. 404-429). Cambridge, UK: Cambridge University Press.

Boesch, C. & Boesch, H. (1984). Mental map in wild chimpanzees: An analysis of hammer transports for nut-cracking. *Primates, 25*(2), 160-170.

Byrne, R. W. (1997). The technical intelligence hypothesis: An alternative evolutionary stimulus to intelligence? In A. Whiten & R. W. Byrne (Eds.), *Machiavellian Intelligence II: Extensions and Evaluations* (pp. 289-311). Cambridge, UK: Cambridge University Press.

Byrne, R. W. & Byrne, J. M. E. (1991). Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla g. beringei*). *Cortex, 27*, 521-546.

Byrne, R. W. & Byrne, J. M. E. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): Variability and standardization. *American Journal of Primatology, 31*, 241-261.

Call, J. & Tomasello, M. (1996). The effect of humans on the cognitive development of apes. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into Thought: The Minds of the Great Apes* (pp. 371-403). Cambridge, UK: Cambridge University Press.

Cant, J. G. H. (1987). Positional behavior of female Bornean orangutans (*Pongo pygmaeus*). *American Journal of Primatology, 12*, 71-90.

Case, R. (1985). *Intellectual Development from Birth to Adulthood*. Orlando, FL: Academic.

Cheney, D. L. & Seyfarth, R. M. (1990). *How Monkeys See the World*. Chicago: University of Chicago Press.

Chevalier-Skolnikoff, S., Galdikas, B. M. F., & Skolnikoff, A. (1982). The adaptive significance of hither intelligence in orangutans: A preliminary report. *Journal of Human Evolution, 11*, 639-652.

Davey, G. (1989). *Ecological Learning Theory*. London: Routledge.

Fischer, K. W., Bullock, D. H., Rotenberg, E. J., & Raya, P. (1993). The dynamics of competence: How context contributes directly to skill. In R. Wozniak & K. W. Fischer (Eds.), *Development in Context* (pp. 93-117). Hillsdale, NJ: Erlbaum.

Fleagle, J. G. (1984). Primate locomotion and diet. In D. Chivers, B. Wood, & A. Bilsborough (Eds.), *Food Acquisition and Processing in Primates* (pp. 105-117). New York: Plenum.

Fox, E. A., Sitompul, A. F., & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In S. T. Parker, R. W. Mitchell & H. L. Miles (Eds.), *The Mentalities of Gorillas and Orangutans* (pp. 99-116). Cambridge, UK: Cambridge University Press.

Fredriksson, G. (1995). *Reintroduction of Orangutans: A New Approach*. Unpublished M.Sc. thesis, University of Amsterdam.

Gibson, K. R. (1993). Tool use, language and social behavior in relationship to information processing capacities. In K. R. Gibson & T. Ingold (Eds.), *Tools, Language and Cognition in Human Evolution* (pp. 251-69). Cambridge: Cambridge University Press.

Hirschfield, L. A. & Gelman, S. A. (1994). Toward a topography of mind: an introduction to domain specificity. In L. A. Hirschfield & S. A. Gelman (Eds.), *Mapping the Mind: Domain Specificity in Cognition and Culture* (pp. 3-35). Cambridge, UK: Cambridge University Press.

Jones, D. L. (1995). *Palms Throughout the World*. Washington, DC: Smithsonian Institute Press.

Kaplan, G. & Rogers, L. (1994). *Orang-Utans in Borneo*. Armidale, NSW: University of New England Press.

Kitahara-Frisch, J., Norikoshi, K. & Hara, K. (1987). Use of a bone fragment as a step towards secondary tool use in captive chimpanzee. *Primate Report, 18*, 33-37.

Langer, J. (1996). Heterochrony and the evolution of primate cognitive development. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into Thought: The Minds of the Great Apes* (pp. 257-77). Cambridge, UK: Cambridge University Press.

Matsuzawa, T. (1991). Nesting cups and metatools in chimpanzees. *Behavioral and Brain Sciences, 14,* 570-571.

Matsuzawa, T. (1994). Field experiments on use of stone tools in the wild. In R. Wrangham, W. C. McGrew, F. B. M. de Waal, P. Heltne, & L. A. Marquardt (Eds.), *Chimpanzee Cultures* (pp. 351-370). Cambridge, MA: Harvard University Press.

Matsuzawa, T. (1996). Chimpanzee intelligence in nature and in captivity: Isomorphism of symbol use and tool use. In W. C. McGrew, L. Marchant, & T. Nishida (Eds.), *Great Ape Societies* (pp. 196-209). Cambridge, UK: Cambridge University Press.

McGrew, W. C. (1992). *Chimpanzee Material Culture.* New York: Cambridge University Press.

Meinel, M. R. (1995). *Eliciting True Imitation of Object Use in Captive Orangutans.* Unpublished BA thesis, Glendon College-York University, Toronto.

Miles, H.L. (1978). Conversations with Apes: The Use of Sign Language with Two Chimpanzees. Unpublished PhD Dissertation, Yale University.

Miles, H. L., Mitchell, R. W., & Harper, S. E. (1996). Simon says: The development of imitation in an enculturated orangutan. In *A.* E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into Thought: The Minds of the Great Apes* (pp. 278-299). Cambridge, UK: Cambridge University Press.

Miles, H. L. (1999). Symbolic communication with and by great apes. In S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.), *The Mentalities of Gorillas and Orangutans* (pp. 197-210). Cambridge, UK: Cambridge University Press.

Mitchell, R. W. (1994). Primate cognition: simulation, self-knowledge, and knowledge of other minds. In D. Quiatt & J. Itani (Eds.), *Hominid Culture in Primate Perspective* (pp. 177-232). Nivet, CO: University Press of Colorado.

Morris, D. (1962). *Biology of Art.* London: Methuen & Co.

Parker, S. T. (1996). Apprenticeship in tool-mediated extractive foraging: the origins of imitation, teaching and self-awareness in great apes. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into Thought: The Minds of the Great Apes* (pp. 348-370). Cambridge, UK: Cambridge University Press.

Parker, S. T. & Gibson, K. R. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. *Journal of Human Evolution, 6,* 623-641.

Parker, S. T. & McKinney, M. L. (1999). *Origins of Intelligence: The Evolution of Cognitive Development in Monkeys, Apes, and Humans.* Baltimore: The Johns Hopkins University Press.

Peters, H. (1995). *Orangutan Reintroduction? Development, Use and Evaluation of a New Method: Reintroduction.* Unpublished M.Sc. thesis, University of Groningen, The Netherlands.

Piaget, J. (1952). *The Origins of Intelligence in Children.* New York: Norton.

Piaget, J. (1954). *The Construction of Reality in the Child.* New York: Norton.

Piaget, J. (1962). *Play, Dreams, and Imitation.* New York: Norton.

Poti', P. (1996). Spatial aspects of spontaneous object grouping by young chimpanzees (*Pan troglodytes*). *International Journal of Primatology, 17,* 101-116.

Povinelli, D. J. (1993). Reconstructing the evolution of mind. *American Psychologist, 48,* 493-509.

Povinelli, D. J. & Cant, J. G. H. 1995. Arboreal clambering and the evolution of self-conception. *Quarterly Review of Biology, 70*(4), 393-421.

Premack, D. (1984). Possible general effects of language training on the chimpanzee. *Human Development, 27,* 268-81.

Reynolds, P. C. (1991). Structural differences in intentional action between humans and chimpanzees--and their implications for theories of handedness and bipedalism. In M. Anderson & F. Merrell (Eds.), *Semiotic Modeling* (pp. 19-46). Berlin: Walter Gruyter & Co.

Rumbaugh, D. M. & Pate, J. L. (1984a). The evolution of cognition in primates: A comparative perspective. In H. Roitblat, T. Bever, & H. Terrace (Eds.), *Animal Cognition* (pp. 569-587). Hillsdale, NJ: Erlbaum.

Rumbaugh, D. M. & Pate, J. L. (1984b). Primates' learning by levels. In G. Greenberg & E. Tobach (Eds.), *Behavioral Evolution and Integrative Levels* (pp. 221-240). Hillsdale, NJ: Erlbaum.

Rumbaugh, D. M., Savage-Rumbaugh, E. S., & Sevcik, R. A. (1994). Biobehavioral roots of language: A comparative perspective of chimpanzee, child, and culture. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee Cultures* (pp. 319-334). Cambridge, MA: Harvard University Press.

Russon, A. E. (1996a). Imitation in everyday use: the nature of spontaneous imitation in free-ranging rehabilitant orangutans. In Russon, A. E., Bard, K. A. & Parker, S. T. (Eds.). *Reaching into Thought: The Minds of the Great Apes.* Cambridge, UK: Cambridge University Press.

Russon, A. E. (1996b). *Report on Release Group VI.* Report to Wanariset Orangutan Reintroduction Project, Wanariset-Samboja, E. Kalimantan, Indonesia.

Russon, A. E. (1998). The nature and evolution of orangutan intelligence. *Primates, 39,* 485-503.

Russon, A. E. (1999). Orangutans' Imitation of tool use: A cognitive interpretation. In Parker, S.T., Mitchell, R.W., & Miles, H. L., (Eds.), *Mentalities of Gorillas and Orangutans* (pp. 119-145). Cambridge, UK: Cambridge University Press.

Russon, A. E. & Bard, K. A. (1996) Exploring the minds of the great apes: Issues and Controversies. In Russon, A. E., Bard, K. A. & Parker, S. T. (Eds.). *Reaching into Thought: The Minds of the Great Apes.* Cambridge, UK: Cambridge University Press.

Russon, A. E., Bard, K. A., & Parker, S. T. (Eds.) (1996). *Reaching into Thought: The Minds of the Great Apes.* Cambridge, UK: Cambridge University Press.

Russon, A. E. & Galdikas, B. M. F. (1993). The complexity of orangutan tool use. XXIII International Ethological Conference, Torremolinos, Spain, Sept. 1-9.

Russon, A. E., Mitchell, R. W., Lefebvre, L. & Abravanel, E. (1998). The evolution of imitation. In J. Langer & M. Killen (Eds.), *Piaget, Evolution and Development* (pp. 103-143). Hillsdale, NJ: Erlbaum.

Russon, A. E. & Susilo, A. (1999). The effects of drought and fires on orangutans reintroduced to Sungai Wain Forest, East Kalimantan, Indonesia. International Ministry of Forests and Estate Crops-Tropenbos Wanariset Technical Report nr. 1999-2, Wanariset-Samboja, Indonesia.

Sakura, O. & Matsuzawa, T. (1991). Flexibility of wild chimpanzee nut-cracking behavior using stone hammers and anvils: An experimental analysis. *Ethology, 87,* 237-248.

Tomasello, M. & Call, J. (1997). *Primate Cognition.* New York: Oxford University Press.

Tomasello, M., Savage-Rumbaugh, E. S. & Kruger, A. (1993). Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Development, 64,* 1688-705.

Toth, N., Schick, K. D., Savage-Rumbaugh, E. S., Sevcik, R. A., & Rumbaugh, D. M. (1993). Pan the tool maker: investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). *Journal of Archaeological Science, 20,* 81-91.

Visalberghi, E. & Fragaszy, D. (1990). Do monkeys ape? In S. T. Parker & K. R. Gibson (Eds.), *"Language" and Intelligence in Monkeys and Apes* (pp. 247-273). New York: Cambridge University Press.

Whiten, A. (1996). Imitation, pretense, and mindreading: secondary representation in comparative primatology and developmental psychology? In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into Thought: The Minds of the Great Apes* (pp. 300-324). Cambridge, UK: Cambridge University Press.

Whiten, A. & Byrne, R.W. (1991). The emergence of metarepresentation in human ontogeny and primate phylogeny. In A. Whiten (Ed.), *Natural Theories of Mind* (pp. 267-282). Oxford: Basil Blackwell.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. (1999). Cultures in chimpanzees. *Nature, 399*, 682-685.

Wrangham, R., McGrew, W. C., de Waal, F. B. M. & Heltne, P. G. (Eds.). (1994). *Chimpanzee Cultures.* Cambridge, MA: Harvard University Press.

Wright, R. V. S. (1972). Imitative learning of a flaked tool technology–the case of an orangutan. *Mankind, 8,* 296-306.

Yamakoshi, G. & Sugiyama, Y. (1995). Pestle-pounding behaviour of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behaviour. *Primates, 36*(4), 489-500.

STUDIES OF TEMPERAMENT IN SIMIAN PRIMATES WITH IMPLICATIONS FOR SOCIALLY MEDIATED LEARNING

Hilary Box
University of Reading, UK

ABSTRACT: The functions of social learning concern the acquisition of skills and information that enable individuals to adjust competently to their environments. However, individuals differ in the extents to which they cope with, maintain and create social and other environmental opportunities. Hence, it is relevant to consider dispositions of individuals interactively - as with emotion, attention and activity; to emphasise self regulatory behaviour, as with selective attention towards or away from environmental conditions. These propensities facilitate positive and negative responses that are associated with the uptake and use of skill and information from other individuals. In these regards, the study of temperament has fertile but mainly unexplored potential. Examples are given from studies of simian primates in which differences in temperament have predictive implications for social learning. When relatively fearful animals confront challenging situations, they are likely to avoid them and become physiologically disturbed. Less fearful and active animals interact more, and in emotionally more positive ways with other individuals. They are more likely to maintain closer physical proximity to others, to attend more to what they are doing and where. Hence, they have greater chances of facilitating advantageous responses - as in feeding strategies. In the acquisition of social skills, less fearful animals engage in play activities more than relatively fearful animals. Such interactions facilitate the development of information about other individuals, and the quality of social behaviour that is developed. These examples show the value of an integrative approach to behavioural studies - in which behaviour is considered with other biological systems.

The aim of this paper is to discuss interactions between two key areas in behavioural biology – with simian primates as examples. One area refers to studies of individual differences with more specific reference to the domain of temperament, the other area is that of socially mediated learning. Temperament is undoubtedly a very broad concept but it may be described generally as the characteristic style of emotional and behavioural response of an individual in a variety of different situations (Prior, 1992) that is often, but not invariably,

---

demonstrated very early in life. It is the stance that an individual takes towards its environment across time and situations. It refers to styles of responsiveness and not to specific acts. It involves both behavioural and other biological correlates of responsiveness to unfamiliar and challenging environmental events in all aspects of the environment - both animate and inanimate. Hence, it influences the ways in which individuals cope with everyday environmental events and the competence of their natural development.

Socially mediated learning may be described as the acquisition of information and skill (at least to some extent) from the behaviour and/or products of other individuals (Box, 1984; Heyes, 1994). Let us consider straight away why looking interactively at studies of temperament and socially mediated learning is important. Hence, the functions of social learning concern information that enables individuals to adjust competently to the demands of their environments. Moreover, developmental competence in this regard involves, for example, both physiological (as with emotional) and behavioural (as with activity and exploration) responsiveness to the challenging conditions of the social and physical environment. Behavioural and physiological measures are interactive;   animals of significantly different biobehavioural dispositions react with their environments, and learn different things about those environments in different ways. In other words, individuals differ in the extents to which they cope with, maintain and create social and other environmental opportunities, and these are propensities that facilitate positive and negative responses that are associated with the acquisition and use of skill and information from other individuals. In these regards, the study of temperament has fertile but as yet mainly unexplored potential (Box, 1999). Moreover, one of many good reasons for taking examples of primates (in this way) is that there has been so much emphasis upon the potential influences of mental abilities on social learning, but relatively little upon interactions among emotional, motivational and social influences (eg Box, 1994). Importantly, studies of differences among individuals in these areas will encourage potentially new domains of understanding in social learning, and generate hypotheses for research.

Further, the primates are an interesting group with reference to studies of socially mediated learning for many reasons. For example, young primates of the two hundred and fifty or so species of living primates live in many different habitats in predominantly tropical and subtropical regions. As a group, they also eat many different kinds of foods, and although there are species that primarily select insects, fruits and flowers or foliage, and are thus relatively specialised in their diets, many species are rather loosely described as 'generalist omnivores'.

Hence, they have a good deal to learn from others about what foods to eat.

Primates are also born into a wide diversity of social organisational systems; they may live predominantly with their mothers, in family groups or in units that are made up of many individuals. Primate social systems include some of the most complex among mammals. Further, compared with most other mammals of similar body size, simian primates have large brains, long lifespans, long interbirth intervals, complex modes of parental care, and long prereproductive phases of development, as in periods of adolescent sterility (Eisenberg, 1981) that may provide opportunities for acquiring skill and information in socially mediated ways. Moreover, behavioural development among such animals continues over their lifespan, and involves the continual adjustment of individuals to the diversity of social and ecological features of their environments. In all, there is much to learn about the social complexities of the species, about gender and age, about co-operative and competitive behaviour, about mating and rearing offspring, about avoiding potential hazards such as predators and harsh weather, and about obtaining food and other maintenance behaviours. Mistakes can be very costly. Therefore it is important to consider the relative extents to which individuals cope with, and create environmental opportunities.

STUDIES OF TEMPERAMENT

The study of temperament in human behaviour has a very long history – over centuries; it has also included interest in both behavioural and other biological correlates (Rothbart, 1989). There are many well known studies with children (Kagan et al, 1992) for instance, that describe distinct and opposite clusters of measures of responsiveness that are based around approach and avoidance to challenging situations, as when children are confronted with unfamiliar surroundings and/or people.

Studies of temperament also cover a very wide range of animal groups; they include fish (eg Francis, 1990; Budaev, 1997) and octopus (Mather and Anderson, 1993). Among mammals well-known observations of individual differences in temperament within wolf litters have been associated with predatory success and social status, for example (Fox, 1972). Breeds of dogs have been extensively studied for temperamental differences among them (Scott and Fuller, 1965; Goddard and Beilharz, 1985; Willis, 1995). There has also been

selective breeding, as for emotional responsiveness, among species of rodents (eg. Gray, 1971).

Moreover, among monkeys there is a growing and substantive literature to support a sound framework within which consistent differences in behavioural and physiological responsiveness to environmental events may be described both within and among species (Clarke and Boinski, 1995). For example, rhesus monkeys have been used a good deal in this area, and with a variety of environmental challenges; they have been studied intensively in captivity singly as individuals, and in social groups. They are also increasingly studied in nature in this domain. Further, among the variety of measures that may be taken to assess temperamental responsiveness in such animals, differences in physiological responsiveness as in the hypothalamic – pituitary axis and the sympathetic nervous system are commonly used (cf. Higley and Suomi, 1989). More specifically, physiological reactivity is often measured by heart rate variability, cortisol and by central amines such as norepinephrine and serotonin. Reactive individuals physiologically, are much more likely to have significantly higher baseline levels in the turnover of catecholamines – especially norepinephrine, and to have higher, less variable heart rates than unreactive individuals. Behaviourally, individual rhesus monkeys that are reactive, are less likely to approach the unfamiliar; they have longer latencies to respond when they do approach; they are more inhibited socially and less likely to initiate social interactions with unfamiliar animals. In brief, they are more fearful and less likely to attempt all forms of challenges in their environments. It is also important for studies of socially mediated learning, for example, that significant differences in temperamental responsiveness may be identified at the time when young monkeys begin to leave their mothers and explore their environments; these differences are stable over time and situations (Suomi, 1991).

Moreover, although the majority of young monkeys within both wild and captive populations of rhesus, explore and take interest in a whole range of unfamiliar conditions, to which they also respond with minimal physiological arousal and show less intensity of behavioural responses, some 20% of the monkeys with the same background and environmental conditions, show consistent behavioural disruption and elevated physiological responsiveness. These monkeys are behaviourally withdrawn in initial interactions with their age mates; they are reluctant to leave their mothers, and explore their environments less. They show withdrawal and behavioural depression to events such as maternal separation. By contrast, individuals that are not reactive

and behaviourally inhibited begin to move away from their mothers earlier. They stay away for longer, and at greater distances; they take advantage of new inanimate situations. Further, individuals that move away from their mothers earlier are usually also those that are first to initiate interactions among their peers when they first meet them (cf. Suomi, 1997).

In addition to the 20% or so of animals that was just mentioned, there is another subgroup of monkeys that account for an additional 5 – 10% of a population that is generally described as impulsive, and particularly in the context of aggressive interactions. Critically, these individuals have low concentrations of central nervous system serotonin activity. There is a whole area of developing research here but we may just note at this point that these are individuals that are impulsive risk takers - as in play, in aggressive and locomotor behaviour;   they migrate earlier than normal, are less social and lack social skills;   they lack social support and seem less able to regulate their behaviour. There are clearly various implications for behavioural development. There are also increased physical risks as with injuries such as falls and fights and, unsurprisingly, there are relatively high mortality rates (cf Suomi, 1997).

IMPLICATIONS FOR STUDIES OF SOCIALLY MEDIATED LEARNING

The information given so far is intended to draw attention to aspects of differences among groups of individuals in such a species, in which biobehavioural dispositions influence responses to environmental events. It is not meant to imply specific generalizations across species but to point up the systems of responsiveness that are involved among such animals. We may now begin to consider natural contexts of behavioural development in which studies of temperament have implications for socially mediated learning and, in particular, with reference to mediating processes in social learning. For example, social attention is critical for social learning; it provides means whereby individuals may take advantage of the information that is available from other individuals, and learn to regulate their behaviour with reference to others. Very young infants are vulnerable and inexperienced, and although in some species such as marmosets and tamarins (Callitrichidae) they are cared for by members of their social groups in addition to their mothers (Yamamoto 1993), the vast majority of infant monkeys and apes are directly dependent upon their mothers for protection against environmental hazards, as well as for their

transportation and nutritional needs. The constant intimate contact in which infants are carried during all the daily activities of their caretaker(s) has important consequences in providing opportunities for socially mediated learning. For example, a young infant may view all its social and ecological environment with close reference to the responsiveness of its mother; in clinging to her ventrum it has access to information by her consistent involuntary responses to environmental events. Pereira and Altmann (1985) in discussing simian species suggest that "the infant probably also becomes sensitive to its mothers tension or calm in social and other situations and becomes conditioned to these contingencies ......" (p.231).

The world of totally dependent infants is gradually interspersed with the acquisition of more independent activities. For example, these are animals in which there is a long period of overlap when infants are both taking their mothers milk, as well as acquiring the digestive tolerance for, and selection of food, together with the skills for feeding independently. There have been pertinent observations of socially mediated feeding at this stage (Whitehead, 1986). The period before nutritional independence is also that in which infants begin to explore the environment; there are opportunities not only to gain information about foods, but about interactions with other individuals. Around eighty per cent of infant rhesus monkeys, for example, are born in a period of two to three months. Hence, each infant has many other monkeys of around the same degree of social and physical competence with which to interact. Once again, the mother is of major importance, and there is frequent emphasis upon her role in providing a secure base of emotional attachment from which an infant may explore and learn about its environment. Moreover, Boccia and Campos (1987) emphasise that in order to act as a secure base, the mother also serves as a reliable source of information about how to respond to the environment. They consider that from an infant's perspective, it is advantageous to acquire information about conditions that create uncertainty. We may refer to this process generally as "social referencing". Hence, by acquiring information, an infant, in this case, gains both knowledge about the environment, and the emotional security to act upon it. It is also an advantage to the mother to attract the attention of her infant and communicate information about environmental events – as in dangerous situations. There are experiments that are directly relevant to this issue. For example, experiments by Boccia and Campos (1987) manipulated positive and negative emotional responses of human mothers to strangers. These were found to significantly influence the responses of their offspring in

the same affective direction. The results showed that infants monitored the affective signals of their mothers and appeared to regulate their responses to a stranger both in expressive and attentional behaviour. This is important because monitoring and/or soliciting information about the social environment will influence socialization. There have been few studies on social referencing among monkeys and apes, but there are some stimulating results for further work. For instance, Evans and Tomasello (1986) found that young captive common chimpanzees (*Pan troglodytes*) discriminated the relationships of their mothers with other adult females of the social group, and adjusted their own behaviour to them accordingly.

Importantly, experiments in this domain provide useful means whereby we can study the acquisition of social information among primate species. There is so much emphasis upon the acquisition of skill such as in foraging strategies, but relatively little upon the acquisition of social information. This is an important omission for species that live in long lasting social groups with relatively complex patterns of social interaction that are central to their life strategies. For all studies of the acquisition of skill and information however, questions that refer to differences in temperamental disposition add further perspectives. As we have noted for instance, reactive and behaviourally inhibited infants interact with their mothers in ways that are different from those monkeys that are relatively unreactive and behaviourally uninhibited. Infants 'use' their mothers differently in her potential 'role' of providing a secure base in emotional security and in providing relevant information. For example, unreactive and unhibited individuals move away from their mothers earlier; they stay away longer; they also take advantage of new situations , and initiate social interactions when they first come across unfamiliar individuals. Interestingly, much may depend upon the disposition of the mother, but it is an advantage of being an outgoing – unfearful individual to develop greater behavioural flexibility in coping with environmental events; to have a wider potential network of social information in dealing with the social and physical environment. By some contrast reactive, inhibited individuals may well be animals that are at risk from other members of their social group. Hence, there are clear advantages in their reluctance to leave their mothers. They may depend upon the information that she provides as well as upon her immediate protection.

Infants cease to be infants and become juveniles when they obtain food, avoid hazards such as predators and keep up with their group – independently (Pereira and Altmann, 1985). Although they do maintain relationships with their caretakers for some time, they gradually become

independent members of their social groups. Their predominant behaviour involves exploring their environment and playing socially. Importantly, individuals are still relatively inexperienced about their physical and social environments, a situation that is compounded by the fact that they have relatively little social support. Unsurprisingly, there are still considerable risks of mortality during the early phase of the juvenile period. Hence, it is critical at this stage to acquire skills for survival that include knowledge about, and avoidance of, hazards such as predators. In later juvenilehood, developing skills, particularly the social skills that are required for success as an adolescent and as an adult, become particularly important, and are gradually developed (Pereira and Altmann, 1985).

For a physically independent but naïve animal, learning how to deal with the environment is facilitated by proximity to experienced individuals. In many situations, social attention depends upon physical proximity among individuals. For instance, Coussi-Korbel and Fragaszy (1994) emphasise that tolerance of spatial proximity supports visual observation of both the affect and activities of other individuals, together with physical access to the places and objects that are used by the other animals. When primate infants are very young they are carried by, and subsequently follow their mothers into proximity with sources of food, resting places and other animals. Gradually, infants determine independently the time that they spend in proximity and interactions with their social and physical environment. Critically then, spatial proximity involves seeking and tolerating, inter-individual distances within which information may be communicated. Hence, once again, differences among individuals in temperamental dispositions are important in creating opportunities for socially mediated learning. Individuals that are bolder and less reactive will have advantages from both seeking and tolerating physical proximity with others – they will do this more frequently, in more positive emotional responsiveness, and at an earlier time. For example, Pereira and Altmann (1985) note that apart from gaining physical protection per se, time spent by young juveniles in proximity to adults provides a context in which they may readily react to, and learn about the alarm and cautious behaviour of adults in dangerous situations. Further, because younger juveniles are permitted close proximity to older experienced animals, they are able to feed on high quality food patches and learn "to identify and process different food items" (p.240).

Discussion about activities of social play in the development of physical and social competence are familiar in behavioural biology. In socially mediated learning play provides opportunities for individuals to

gain information about other individuals as individuals, as well as about patterns of social interaction.   There are significant quantitative differences among species, and with individuals of different age and gender in different ecological and social conditions.   Young rhesus monkeys begin to associate mainly with their own gender in play activities from around four to five months old (Suomi, 1991).   This continues throughout the second year of life.   Males engage in much rough and tumble play with all monkeys that will participate.   However, females stop participating in rough and tumble play from about six months old, and they rarely initiative such activities.   They spend more time in grooming and chasing with other females, and competitive behaviour among them relates critically to competition for food as critical ecological constraints in their reproductive success. Furthermore, as young females grow older into adolescence, they play very little and then, mainly with young juveniles and infants.   By contrast, young males continue to play well into their adolescence, predominately with their age-sex peers and thereby continue to develop their competitive skills. Further, when rhesus monkeys are about four months old their bouts of play are very short; they occur with one other animal, and with very simple behavioural sequences.   Later on, at between two and three years of age, social play occupies a similar amount of time but occurs in much longer bouts, and frequently engages two or more animals. Social play is very much more complex in which coalitions among individuals are formed and reversed. Play includes elementary forms of behaviour that are used by adults to coordinate a variety of social and reproductive behaviour (Suomi, 1991). Hence, play behaviour provides information for socially mediated learning in various natural contexts. Importantly, there are good indications that differences among individuals in the extents to which they play spontaneously in later infancy, are predictive of such differences into childhood and adolescence; further, that play behaviour is inhibited by patterns of responsiveness that are more reactive and behaviourally inhibited (Higley, 1985).   Moreover, young monkeys with relatively insecure attachments to their mothers play less often and show less sophisticated patterns of interactions in play than those monkeys that are securely attached (Higley, 1985). Hence, it is important generally with regard to the many opportunities for social learning that play behaviour provides, that less reactive animals engage in more play than reactive ones, and that they are more likely to initiate play activities.

The development of social skills involves a variety of dimensions of social competence that reflect the demands of complex and changing social interactions.   These include competitive and co-operative

strategies; they involve co-operative alliances, reconciliation and social status. A good deal of work is needed here with reference to differences in temperament. However, there are some interesting findings with regard to social status. This is a critical area of social competence that involves priority of access to resources such as food, mates and shelter, that are necessary for survival and fitness. We may note, for example, from various studies in captivity, and in the field, that although we need more detailed information, there is an association between lack of high social status and fearful reactive responsiveness in the work with rhesus monkeys. It has been found in captivity for example (Scanlan, 1987) that reactive animals were more likely to give way, to acquiesce, to other monkeys in social interactions, or in situations where there was competition for resources. Further, that in the field, Rasmussen and Suomi (1989) found that low reactive rhesus males had profiles of behaviour that would facilitate success in competitive interactions. Further, studies of temperamental responsiveness have drawn attention to some interesting complexities. Sapolski's work (eg Sapolski and Ray, 1989; Ray and Sapolski, 1992) on free ranging savannah baboons has shown for example, that high status males include both individuals that have a high reactive style of responsiveness to environment challenge, as well as those that have a low reactive style of responsiveness. In brief, individuals who consistently showed less intense behavioural responses to psychological stressors such as capture – and were also able to distinguish between the salience of their response to different intensities of stressors (such as between the presence of another adult male compared with actually being threatened by him) also had low basal concentrations of cortisol. In contrast, dominant males who were highly reactive to identical stressors had basal cortisol levels comparable to those of subordinate adult males (Sapolski, 1990). This work is very important in showing the potential complexities of clusters of temperamental dispositions in complex behavioural interactions. It also draws attention to interrelations between endocrine activity and styles of social information processing. Moreover, higher levels of stress responsiveness among the high status males that were highly reactive to environmental challenges lowered their immune responsiveness and increased their susceptibility to health hazards as with cardiovascular disease (Sapolski, 1990).

It is obviously critical to the whole development of the area of temperament and socially mediated learning to recognise such complexities. It is also the case however, that we have a variety of information that leads to fruitful hypotheses towards the understanding

and prediction of socially mediated learning that we also need to develop. At this point we may emphasise and recapitulate some of the points that were made earlier. Hence young, unreactive and uninhibited animals as in rhesus monkeys, are more active; they move around and explore more. They also become less disturbed physiologically. In other words, they cope better especially with unfamiliar situations. Importantly, these are responses that increase the probability that less fearful individuals will confront, attend to, and become familiar with previously unfamiliar features of their environments. When relatively fearful individuals confront challenging situations, they are more likely to avoid them and become physiologically disturbed. Moreover, less fearful and active animals interact more, and in emotionally more positive ways with other animals. They are more likely to maintain closer physical proximity to others, to attend more to what others are doing and where. Hence, they may have greater chances of facilitating advantageous responses to environmental challenges – as in feeding strategies. Again, in the acquisition of social skills, less fearful animals engage in play activities more than relatively fearful animals. Such interactions facilitate the development of information about other individuals, and about the quality of a range of social behaviours that is developed. Moreover, it is important to consider that individual variations in temperamental dispositions among animal populations are robust and represent the range of individual differences that has been selected for (eg Wilson, 1998). Hence, it is also important that we should consider the advantages and disadvantages of such variations. It is interesting to consider, for example, that in large socially complex social units such as are found among many species of the simian primates, an extensive range of temperamental dispositions may allow for the exploitation of a wider range of social success, whilst at the same time reducing direct competition among individuals (Clark, 1991).

Differences in temperamental dispositions among species of monkeys also raise functional questions with regard to socially mediated learning. There is not a large number of studies but there are some interesting hypotheses. Species have been studied with a variety of unfamiliar social and inanimate challenges. Moreover, there are robust data to support hypotheses that associate interrelationships among species typical temperamental responses with their social and ecological systems (Clarke and Boinski, 1995). As with the findings for individuals within species, the shy-bold/reactive-unreactive dimensions of comparison are apparently the most appropriate (Clarke and Boinski, 1995).

Tentative hypotheses for such differences include defence against

predation, feeding and habitat specialisations. Clarke and Boinski (loc cit) note for example, the hypothesis that species that are more curious, bold, unfearful and instrumental in their approach to unfamiliar situations are also those that utilise relatively high energy foraging strategies and/or complex foraging, and tend to have 'omnivorous' diets. Given the emphasis that has been placed upon rhesus monkeys in this paper, it is interesting to consider comparisons among species of the same genus (*Macaca*). Moreover, the macaques are potentially a good model for such comparisons. Hence, the twenty or so species live in many different habitats across Asia; they eat many different foods (Melnick and Pearl, 1987); there are also differences in ranging behaviour, habitat use and foraging behaviour, and there are differences in sexual and social behaviour (cf. Clarke and Boinski, 1995). Interestingly, there is now good evidence on the basis of a variety of social and inanimate challenges, that a number of species are behaviourally and physiologically distinct (eg. Clarke and Mason, 1988; Clarke *et al.*, 1988; Clarke and Lindburg, 1993; de Waal, 1989; Thierry, 1985). Responsiveness varies greatly in different challenging situations. There are significant interspecific variations, for example, in aggressiveness, in reconciliatory behaviour, in curiosity and exploratory behaviour. Hence, among a number of species of the macaques, rhesus monkeys are bold and unreactive in their approach to unfamiliar environmental events. They are relatively exploratory; they are the most aggressive and the least conciliatory; they are less passive socially. Interestingly, this is a species that is very widely distributed, and thrives in a diversity of ecological conditions . It is interesting to consider for instance, that individuals that are relatively reactive, and inhibited, may be comparatively disadvantaged in such a species.

Comparative studies among the macaques also serve to highlight the influence of 'social support' in behavioural development namely, the amount of affiliative behaviour directed towards an individual (Boccia *et al.*, 1997). Bonnet macaques (*M. radiata*), for example, have a different social developmental network than pigtail macaques (*M. nemistrina*) with which they are often compared. Bonnet monkeys have a relatively open social system; mothers are less restrictive and infants interact freely and frequently with numbers of group members. Social attachments are formed with more individuals than among young pigtail monkeys. There are immediate implications for social learning. Differences in social networks are important for routes of transmission of behaviour, as in social attention to a wider social nexus, that also provides information about the environment in affiliative contexts. Moreover, individuals of these two species respond differently -

physiologically and behaviourally to environmental challenges. Importantly,the natural availability of alternative social attachments can modulate against the physiological and behavioural consequences of aversive events. Further, infant bonnet monkeys without such social support are not buffered against adverse environmental events. The critical point is that the different social organisational style of bonnet monkeys provides the opportunity to ameliorate expressions of negative responsiveness,and provides increased opportunities for socially mediated learning of positive responsiveness to environmental events. Social support both modulates physiological responsiveness and facilitates social attachment, which in turn may facilitate security, exploration and exposure to information that is available from other group members. We might also note that social opportunities of social support not only influence the ability of individuals to cope with their environments, but to remain healthy and reproductively fit. Hence, there are also issues that are relevant to health, welfare and conservation in both natural and captive conditions. For example, developing research in the field of psychoneuroimmunology is of interest in this context (eg Laudenslager and Boccia, 1996).

In conclusion, the examples given in this paper draw attention to differences in biobehavioural dispositions that influence learning in a variety of contexts. The fact that they have not been considered with reference to familiar discussions of animal social learning is an omission in our thinking in this area.

The point is that the interrelationships among biobehavioural propensities within individuals of different species have implications for their opportunities to acquire and use skill and information from other animals. Hence, interactive studies among such biobehavioural propensities represent realistic approaches of study in this area, and emphasise that such learning is socially mediated.

ACKNOWLEDGEMENTS

REFERENCES

Boccia, M.L. & Campos, J.J. (1987) Social attentional processes in human and non-human primate infants. *Primate Report, 18*, 3-10.

Boccia, M.L., Scanlan, J.M., Laudenslager, M.L., Broussard, C.L. & Reite, M.L. (1997) Presence of "friends" mitigates behavioral and immunological responses to maternal separation in bonnet macaques. *Physiology and Behavior, Vol 61*, 191-198.

Box, H.O. (1984) *Primate Behaviour and Social Ecology*, Chapman and Hall, London.

Box, H.O. (1999) Temperament and socially mediated learning among primates. In H.O. Box and K.R. Gibson (Eds.), *Mammalian Social Learning: comparative and ecological perspectives* (pp. 33-56). Cambridge University Press.

Box, H.O. (1994) Comparative perspectives in primate social learning: New lessons for old traditions. In J.J. Roeder, B. Thierry, J.R. Anderson and N. Herrenschmidt (Eds.), *Current Primatology* (pp. 321-327). Universite Louis Pasteur, Strasbourg.

Budaev, S.V. (1977) "Personality" in the guppy *(Poecilia reticulata)*: a correlational study of exploratory behavioural and social tendency. *Journal of Comparative Psychology, 111*, 399-411.

Clark, A.B. (1991) Individual variation in response to environmental change. In H.O. Box (Ed.), *Primate Responses to Environmental Change* (pp. 91-110). Chapman and Hall, London.

Clarke, A.S. & Boinski, S. (1995) Temperament in Nonhuman Primates. *American Journal of Primatology, 37*, 103-125.

Clarke, A.S. & Lindburg, D.G. (1993)   Behavioural contrasts between male cynomologous and lion-tailed macaques. *American Journal of Primatology, 29*, 49-59.

Clarke, A.S. & Mason, W.A. (1988) Differences among three macaque species in responsiveness to an observer. *International Journal of Primatology, 9*, 347-364.

Clarke, A.S., Mason, W.A. & Moberg, G.P. (1988) Differential behavioural and adrenocortical responses to stress among three Macaque species. *American Journal of Primatology, 14*, 37-52.

Coussi-Korbel, S. & Fragaszy, D.M. (1995) On the relation between social dynamics and social learning. *Animal Behaviour, 50*, 1441-1453.

de Waal, F.B.M. (1989) *Peacemaking Among Primates.* Harvard University Press, Cambridge, M.A.

Eisenberg, J.F. (1981) *The Mammalian Radiations.* University of Chicago Press, Chicago.

Evans, A. & Tomasello, M. (1986)   Evidence for social referencing in young chimpanzees *(Pan troglodytes)*. *Folia Primatology, 47*, 49-54.

Fox, M.W. (1972) Socio-ecological implications of individual differences in wolf litters: a developmental and evolutionary perspective. *Behaviour, 41*, 298-313.

Francis, R.C. (1990) Temperament in a fish: A longitudinal study of the development of individual differences in aggression and social rank in the Midas Cichlid. *Ethology, 86*, 265-352.

Goddard, M.E. & Beilharz, R.G. (1985) A multivariate analysis of the genetics of fearfulness in potential guide dogs. *Behaviour Genetics, 15*, 69-89.

Gray, J.A. (1971) *The Psychology of fear and stress.* McGaw Hill, Toronto, N.Y.

Heyes, C.M. (1994) Social learning in animals: Categories and mechanisms. *Biological Reviews, 69*, 207-231.

Higley, J.D. (1985) Continuity of social separation behaviours in rhesus monkeys from infancy to adolescence. Unpublished doctoral dissertation, University of

Wisconsin, Madison, WI.

Higley, J.D. & Suomi, S.J. (1989) Temperamental Reactivity in Non-Human Primates. In G.A. Kohnstamm, J.E. Bates and M.K. Rothbart (Eds.), *Temperament in Childhood* (pp. 153-167). John Wiley and Sons Ltd.

Kagan, J., Snidman, N. & Arcus, D.M. (1992) Initial reactions to unfamiliarity. *Current Directions in Psychological Science, 1,* 171-174.

Laudenslager, M.L. & Boccia, M.L. (1996) Some observations of Psychosocial Stressors, Immunity, and Individual Differences in Nonhuman Primates. *American Journal of Primatology, 39,* 205-221.

Mather, J.A. & Anderson, R.C. (1993) Personalities of octopuses (*Octopus rebescens*). *Journal of Comparative Psychology, 107,* 336-340.

Melnick, D.J. & Pearl, M.C. (1987) Cercopithecines in multimale-groups: Genetic diversity and population structure. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker (Eds.), *Primate Societies* (pp. 121-134). University of Chicago Press, Chicago.

Pereira, M.E. & Altmann, J. (1985) Development of social behaviour in free-living nonhuman primates. In E.S. Watts (Ed.), *Nonhuman Primate Models for Human Growth and Development* (pp. 217-309). Liss New York.

Prior, M. (1992) Childhood Temperament. *Journal of Child Psychiatry, 33,* 249-279.

Rasmussen, K.L.R. & Suomi, S.J. (1989) Heart rate and endocrine responses to stress in adolescent male rhesus monkeys on Cayo Santiago. *Puerto Rico Health Science Journal, 8,* 65-71.

Ray, J.C. & Sapolski, R.M. (1992) Styles of male social behaviour and their endocrine correlates among high ranking baboons. *American Journal of Primatology, 28,* 231-50.

Rothbart, M.K. (1989) Biological Processes in Temperament. In G.A. Kohnstamm, J.E. Bates and M.K. Rothbart (Eds.), *Temperament in Childhood* (pp. 77-110). John Wiley and Sons Ltd.

Sapolski, R.M. (1990) Adrenocortical function, social rank, and personality among wild baboons. *Biological Psychiatry, 28,* 862-878.

Sapolski, R.M. & Ray, J.C. (1989) Styles of dominance and their endocrine correlates among wild olive baboons (*papio anubis*). *American Journal of Primatology, 18,* 1-13.

Scanlan, J.M. (1987) Social dominance as a predictor of behavioural and pituitary-adrenal response to social separation in rhesus monkey infants. Paper presented at the meeting of the *Society for Research in Child Development.* Baltimore, MD, April 1987.

Scott, J.P. & Fuller, J.L. (1965) *Dog Behaviour: The Genetic Basis.* University of Chicago Press, Chicago and London.

Suomi, S.J. (1985) Biological response styles: experiential effects. In H. Klas and L.J. Siever (Eds.), *Biologic Response Styles: Clinical Implications* (pp. 2-17). American Psychiatric Press, Washington, DC.

Suomi, S.J. (1991) Uptight and laidback monkeys. In S.E. Brauth, W.S. Hall & R.J. Dooling (Eds.), *Plasticity of Development* (pp. 27-56). MIT Press Cambridge, M.A.

Suomi, S.J. (1997) Early determinants of behaviour: evidence from primate studies. *British Medical Bulletin, 53,* 170-184.

Suomi, S.J., Rasmussen, K.L.R., & Higley, J.D. (1992) Primate models of behavioural and physiological change in adolescents. In E.R. McAnarney, R.E. Kreipe, D.P. Orr & G.D. Comerci (Eds.), *Textbook of Adolescent Medicine* (pp. 135-139). Philadelphia: Saunders.

Thierry, B. (1985) Patterns of agonistic interactions in three species of macaques (*macaca mulatta, M. fascicularis, M. tonkeana*). *Aggressive Behaviour*, *11*, 223-233.

Whitehead, J.M. (1986) Development of feeding electivity in mantled howling monkeys *Alouatta palliata*. In: J.G. Else & P.C. Lee (Eds.), *Primate ontogeny, cognition and social behaviour* (pp.105-117). Cambridge University Press.

Willis, M.B. (1995) Genetic aspects of dog behaviour with particular reference to working ability. In J. Serpell (Ed.), *The Domestic Dog: its evolution, behaviour and interactions with people* (pp. 54-64). Cambridge University Press.

Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London, Series B353*, 199-205.

Yamamoto, , M.E. (1993) From dependence to sexual maturity: the behavioural ontogeny of Callitrichidae. In: A.B. Rylands (Ed.), *Marmosets and Tamarins: Systematics, Behaviour and Ecology* (pp.235-254). Oxford University Press.

SONG STRUCTURE AND FUNCTION OF MIMICRY IN THE AUSTRALIAN MAGPIE (*Gymnorhina tibicen*): COMPARED TO THE LYREBIRD (*Menura ssp.*)

Gisela Kaplan
University of New England, AUSTRALIA

ABSTRACT: This paper compares two species of songbird with the aim of elucidating the function of song and also of mimicry. It attempts to understand why some birds mimic and takes as examples the lyrebird (*Menura sp.*) and the Australian magpie (*Gymnorhina tibicen*). Mimicry by the magpie and its development has been recorded and analysed. The results show that magpies mimic in the wild and they do so mimicking species permanently settled in their own territory. So far 15 types of mimicry have been identified. One handraised Australian magpie even developed the ability to vocalise human language sounds, words and phrases. Results show that mimicry is interspersed into their own song at variable rates, not in fixed sequences as in lyrebirds. In one case it was possible to show an extremely high retention rate of learned material and a high plasticity for learning. Spectrogram comparisons of sequences of mimicry with the calls of the original species, and comparison of magpie mimicry with lyrebird mimicry is made. Both species may justifiably vie for the position of the foremost songbirds of Australia, and both are territorial, yet the function, structure and development of song are different in the two species. It is argued that possible functions of mimicry are related not only to social organisation but also to the niche each species occupies. Territoriality may go some way to explaining the complexity of song but not necessarily the different functions of mimicry or the varying degrees of complexity of communication. We need to ask what conditions may foster development of complex communication patterns in avian species.

INTRODUCTION

Two of the foremost songbirds of Australia, and possibly the world, are the Australian magpie (*Gymnorhina* ssp.) and the lyrebird (*Menura* ssp). Both are also the most prolific Australian mimics in the wild. Until recently, knowledge of mimicry by magpies in the wild was confined to popular knowledge and speculation. Here it is shown that

Address correspondence to Prof. G. Kaplan, Division of Zoology, School of Biological Sciences, University of New England, Armidale, NSW 2351, Australia. e-mail: gkaplan@metz.une.edu.au

the Australian magpie is capable of very complex vocal communication, including carolling and mimicry (Kaplan, 1998). The lyrebird, especially the superb lyrebird (*Menura novaehollandiae*), has one of the most powerful songs of any bird and it is widely known for its spectacular mimicry (Robinson & Curtis, 1996). The purpose of comparing two ancient Australian songbird species is to propose that song structure, including mimicry, may appear to be similar in each species but serve different functions.

Until now it was not possible to compare the song structure of lyrebirds with magpies because too little was known about the mimicry of magpies, or of any other Australian bird using mimicry. Although the magpie has been comparatively well researched in relation to other Australian songbirds, it is still surprising how little systematic work has appeared on the song of the magpie. There exists just one major study of vocalisation in magpies, published in three parts (Brown & Farabaugh, 1991; Brown, Farabaugh & Veltman, 1988; Farabaugh, Brown & Veltman, 1988). Many of the earlier vocalisation data by Robert Carrick and colleagues were never published (Carrick, 1963; Carrick, 1972). This paper reports the incorporation and retention of mimicked sequences, including the human voice, in magpies and lyrebirds. The data of magpies is based on the author's own research, whereas the examples of lyrebird mimicry are drawn from other researchers for comparison only.

Mimicry is not a rare occurrence amongst avian species. In 1934 Chisholm identified 56 Australian avian species with some skills in mimicry (Chisholm, 1948) and since then about half of those identified have been verified by ornithologists. While some forms of mimicry might be impossible due to anatomical limitations (Thorpe, 1961), mimicry appears to be a ubiquitous avian phenomenon. In the 1970s Gramza even postulated that eventually most species of birds will be found to have some ability to copy extra-specific sounds (Gramza, 1972).

The Australian magpie and the lyrebird lend themselves to comparison. Both have an ancient lineage amongst the Australo-Papuan centred corvida (Schodde & Mason, 1999; Sibley & Ahlquist, 1985). Both are territorial and ground feeders and both are capable of producing loud and musical notes that are widely audible. Their frequency range is similar and their skills in and extent of using mimicry are similar, as this paper shows, although the lyrebird, with its three syringeal muscles, rather than the oscines' typical four, is possibly more flexible.

However, the social organisation and the breeding and dispersal strategies of the lyrebird and the magpie differ from one another. The

Australian magpie is an exemplary model for several reasons. Although the female builds the nest alone and incubates the eggs by herself, males and females share in raising the young (Queensland National Parks, 1987). Males may also feed the female during the weeks of incubation. Australian magpies, in common with many other members of the corvidae family (white-winged choughs, apostlebirds, crows, currawongs), have very complex social relationships, reflected in complex vocal communication and, at times, cooperative breeding or hunting (Cockburn, 1996; Farabaugh, Brown & Hughes, 1992; Veltman, 1984). Territoriality, cooperative breeding and hunting (O'Neill & Taylor, 1984) are signs of complex social organisation. These criteria have favoured the development of complex song and communication patterns in both sexes (Brown & Farabaugh, 1991; Brown *et al.*, 1988).

Song, in Australian magpies, is not used specifically for courtship (Brown and Veltman, 1987) and, therefore, sexual competition has not led to a male developing a song that is more elaborate than that of another male, nor does singing bestow an advantage to the male alone (Kaplan, 1998). Moreover, not only do both males and females sing throughout the year, but also duetting occurs between males and females (Brown *et al.*, 1988; Farabaugh, 1982). Male and female singing is, however, not confined to pair duetting or territorial defence. Duetting between males and females is thought to have evolved in dense tropical rain forest habitats, as a means of staying in touch when visual contact may be difficult (Catchpole & Slater, 1995). Such a conclusion cannot be drawn for the Australian magpie, since they are very widespread in open areas and occur across the Australian continent, with the exception for areas of desert (Carrick, 1972). Hence, the species occurs in a wide variety of climate zones. Indigenous to Australia, but also introduced to New Zealand (McIlroy, 1968) and some islands of Fiji (Clunie & Morse, 1984), Australian magpies have adapted to tropical and subtropical regions and they are particularly widespread in temperate zones (Baker, Mather & Hughes, 1995; Burton & Martin, 1976).

By contrast, lyrebirds occupy only a relatively small stretch of the east coast of Australia and live in areas of remaining dry scerophyl and wet forests. Rainforest (whether temperate or subtropical) is its main habitat. There are two species, the superb lyrebird (*Menura novaehollandiae*) with a wide but patchy distribution extending from near Melbourne to the rainforest hinterland of Brisbane. The Albert lyrebird (*Menura alberti*) is now found only in very small patches of rainforest southwest of Brisbane, at the northern border of New South Wales. Males are polygamous and promiscuous and they fertilise

several females in a season (Schodde & Mason, 1999). They take no share in nestbuilding, incubation or in rearing the young but it appears that the young males later take their father as tutor for song-learning. Lyrebirds are scrub-birds and are vulnerable to predation whereas magpies are not. Magpie young disperse far from the parent territory, whereas lyrebird offspring stay close by. Powy's seven-year study found that amongst the superb lyrebird groups studied (seven in all), there was structural, locational and temporal constancy of territorial song from one generation to the next (Powys, 1995). There were also distinct regional dialects which were maintained over generations.

Magpie song has been found to fall into several distinct categories. One category includes the pre-dawn/nocturnal calls. They are relatively stereotyped monotonous songs in the summer months, or, as Sanderson and Crouche argued, during the breeding season only. Another category is the territorial song containing loud individual calls and carolling of two or more magpies. A third is the subsong, an individual song (Sanderson & Crouche, 1993). Mimicry is found only within this third category. There are also a variety of context specific calls (see also Robinson, 1956; Robinson, 1975) that could, conceivably form a fourth category. In lyrebirds, one can distinguish mainly two forms of song: the territorial song and the breeding song. The territorial song may contain percussion sounds and it is shown in this paper that it usually has a relatively simple structure. The breeding song, however, is complex and mimicry is found in the breeding song only (Robinson & Curtis, 1996). There is some suggestion that lyrebirds do not use all their mimicked sounds in the breeding song but only those that are loud and clear (Readers Digest, 1976) but no research has proven or disproven this statement to date.

This paper reports evidence of incorporation of mimicry into magpie song from different regions in Australia for the two subspecies, the black-backed magpie of eastern Australia (G. *tibicen*) and the white-backed magpie of southern and western Australia (G. *hypoleuca*).

METHODS

The study used the vocalisations of 22 magpies, including only those that produced mimicked sounds. Two of them were handraised magpies. These were not the only magpies raised. Of the eighteen magpies that were hand-raised between 1995 and 2000, only two developed mimicry and one of them (Bird A), held in the territory for one year, developed extensive skills in mimicry. For those two mimicking magpies, an aviary was placed near the house and the

observer was unseen by the magpies.   A standard unidirectional microphone was attached to a stand at a height of 1.80 m, situated 20 cm from the main perching branch of each individual bird.   The observer was unseen and a Sony field cassette recorder was operated from inside the house at any time when vocalisations occurred. Vocal development of Bird A was recorded for a period of half a year, with observation times of 12 hours per day for six days a week, dropping to 10 hours per day and 5 days a week after half a year. This study concluded after 12 months and the bird was successfully released. The vocalisations of the other hand-raised mimicking bird (Bird B) were recorded for a period of three months only because it was ready for release after three months of care. Australian magpies, as all native Australian fauna, are a protected species and handraising them can occur only under licence and for the purpose of release. Birds cannot be held beyond the time needed for total recovery. The birds were cared for under licence and the research conformed to the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (1997).

Both birds, in separate aviaries and in different years (Bird A from late 1995 to late 1996 and Bird B from late September 1997 to early December 1997) were held in aviaries under cover but they had ample sunlight each day and access to water and food ad libitum. Initially, both had to be hand-fed at half hour intervals from 6am to 7pm each day.   In the case of Bird A, handfeeding was for a duration of two months, and in the case of Bird B for one month.   Both birds were found within the broad geographical area of the New England Tableland, a temperate climate zone, 1200 m above sea level in north west New South Wales, and they were reared on a property near Armidale.

An extra 20 magpies were part of this study and they were wild magpies and the data were obtained from field sound recordings. The method for obtaining these data had to be unconventional. Mimicry by magpies in the wild is too sporadic for systematic study and is not always witnessed unless accidentally overheard in the field or occurring near human dwellings.   To achieve a wider sample than had been secured in captivity, I was given permission during an interview on the ABC Science Show radio program (on air 28 December 1996) to ask listeners to send in tapes and detailed accounts of whether they had ever heard a magpie mimic.   The response was overwhelming.   Over the next three months well over 100 letters and telephone calls were received.   Only a few respondents had actually recorded the mimicry but these respondents were willing to send their taped information. Some information was not useable due to the quality of the tapes but

nine tapes were suitable for analysis, yielding separate recordings of mimicry (N=9).

These specific mimicked vocalisations by magpies derived from different territories, and hence were assumed to be of unrelated individuals and non-overlapping territories. Recordings used for analysis came from Western Australia (N=1), South Australia (N=1), Victoria (N=3, different townships), New South Wales (N=2, different townships), the Australian Capital Territory (N=1) and Queensland (N=1). Respondents of useable tapes were additionally asked whether they knew the sex and age of the taped individuals and whether any individuals had been hand-raised, were tamed or wild. They were also asked if they knew whether the mimicked species were permanent residents in the magpies' territory. Not one of the recorded birds had been hand-raised and only one was tame enough to take some food supplied by humans. All others were wild and had been in their respective territories for some years. Not all respondents were clear of the sex of the bird they had recorded. In magpies, morphological sex differences are minimal and may, at times, be difficult to identify. It was certain, however, that not one of the recorded birds was a juvenile. Juveniles have different plumage to adults and are therefore easily identified. In every case, the mimicked sounds derived from permanent residents.

In addition, I was able to peruse some of the tapes derived from a study of magpie vocalisations undertaken by John Carrick, Norman Robinson and Bruce Falls in the Canberra area in 1965. These had never been used for publication. The tapes were generously provided by Prof. Bruce Falls (Canada) and they were annotated so that it was possible to establish age and sex and context of the mimics. Thus the total number of analysed mimics derived from other sources came to ten, and the complete sample size was N= 12, including the hand-raised magpies. This is the largest sample of mimicry recordings of magpies.

Mimicry and its development was examined and analysed using the sound analysis program 'Canary', developed by Cornell University. Initially, Canary 1.2 was used and, with a later system, this was changed to Canary 1.2.4, without loss of data to the original recordings. This analysis yielded sound spectrograms and waveforms.

Wherever possible, the mimicked species were recorded separately. This was possible in all cases of the mimicry displayed by the hand-raised magpies, but substitutes had to be found for almost all sounds submitted from around Australia. Spectrogram comparisons of mimicked sequences with the original species and with lyrebird mimicry were made. The lyrebird recordings were those of commercially available recordings from 'Birds Australia'.

The tapes were analysed to find mimicry. It became clear on listening to tapes supposed to contain mimicry that a definition of mimicked sounds was needed. By definition, a bird could not produce mimicry of sounds that fell outside its own physiological vocal range. Just because a vocalisation sounded 'different', it might not necessarily be regarded as mimicry.

The definition of mimicry that was ultimately adopted was derived not just from auditory sampling but from assessing visual images of the sounds in question. Copying was disregarded as mimicry if it occurred only once. 'False' mimicry was classified as brief moments of odd sound modulations that suggested other influences but were not structured sufficiently to be included. There were often suggestions of mimicry which were discarded because they fell into the typical sound structure range of magpies. These were therefore regarded as variations on the species-specific song.

Vocalisations accepted as 'true' mimicry had to fulfill four specific conditions: a sample presented a special pattern of sound that was atypical of the normal structure of magpie song. Second, the pattern had to be repeated and occur again in the song repertoire. Third, in repeating the same structure, a break with its typical species-specific call had to occur and, fourthly, the atypical sound pattern needed to be identifiable as a species-specific pattern of the vocalisations of another species. Only those vocalisations that fulfilled all four variables were then subjected to closer analysis. Identification of sounds involved naming the mimicked species. These were isolated and then also sent to the CSIRO Sound Library in Canberra for separate verification.

RESULTS

From the tapes 15 distinct and easily recognisable types of mimicry were identified. Mammal calls included: horse neighing, dog barking, cat mewing, and human voices. The identification of mimicry of other birds was at times more difficult because recognition required knowledge of the vocal repertoire of a wide range of avian species and because sometimes brief sequences of unusual sounds were not unambiguously those of another species. It is possible that some were missed. The mimicked avian species that were identified in wild magpie vocalisations without any element of doubt were: lapwing, lyrebird, kookaburra, currawong, crimson rosella, eastern rosella, red wattlebird, barking owl, and the boobook owl. Figure 1 gives examples of widely different sound structures of mimicry, one of horse neighing and the other of a boobook owl. Note that the sound of the boobook
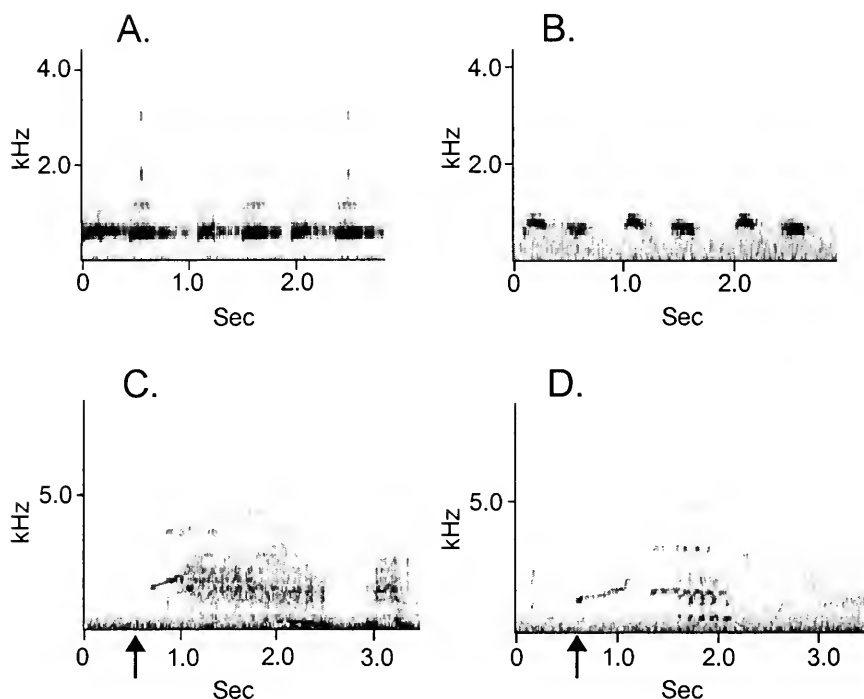
Figure 1.   Sonograms of sounds and their mimicry by wild magpies.   A, Boobook owl; B, Mimicry of boobook owl.   A and B were recorded in northwest New South Wales, Australia; C, Horse neighing; D, Mimicry of horse neighing recorded in Ararat, a town in Victoria, Australia.   Arrows in C and D indicate the spikes of sound at the start of the neighing.

owl (not a songbird) is characterised by heavy hooting, largely consisting of noise (hence the broad line).   The magpie mimicked this owl very adequately by attempting to stay in the same frequency range (under 1 kHz) and broadly copying the noise.   There are no overtones in this rendering.   By contrast, the mimicry of the horse neighing is rich in overtones.   While it is more musical (clear formants rather than the fuzzy noise of the horse), the magpie has rather faithfully reproduced the structure of the sound.   Captive birds also mimicked budgerigars and peachface parrots.

The hand-raised magpies (Birds A and B) yielded 70 hours of vocalisations.   Table 1 shows an analysis of species calls that were mimicked by these magpies.   (Note that Table 1 excludes all resident small avian species with calls above the frequency range of magpies such as pardalotes, European gold finches, superb blue wrens, silver eyes, several species of robin, eastern spinebills, grey fantails, whitebrowed scrub wren, weebill, house sparrows, white-throated

Table 1. Vocalising species on the property in which Bird A was reared
and maintained for 1 year. Note that this bird mimicked only those species
that were in close proximity to its own aviary and that were permanent
residents on the property. The species listed excludes all resident small
avian species with calls above the frequency range of magpies. P,
permanent; VR, visitor - regular; VS, visitor - seasonal or seldom.

Source of Sound	Vocalising species on territory	Mimicked	Status of vocalising species
Near Sounds (heard and seen)	Kookaburra	√	P
	Peachface parrots	√	P
	Budgerigars	√	P
	Magpies	√	P
	Dogs	√	P
	Human voices	√	P
	Crimson Rosella	-	VR
	Eastern Rosella	-	VR
	Galahs	-	VR
	Red wattlebirds	-	VR
	Grey butcherbird	-	VS
	Currawongs	-	VS
	Magpie larks	-	VS
Distant sounds (heard but not seen)	Car horns	-	
	Engine sounds	-	
	Lapwings	-	
	Donkeys	-	

gerygone, southern whiteface, and other species that either rarely
vocalise or were very rarely seen such as the sacred kingfisher,
goshawk, kestrel, crested pigeon, white-backed swallows, feral pigeons,
red-rumped parrots and dollarbirds). The analysis of mimicked species
showed that not all sounds were copied but only those of significant
fauna that permanently shared the same territory as the magpie. These
included other captive birds housed near the magpies and household
pets, human carers but not any wild species that visited the vicinity of
the cages (Table 1).

Certain mimicked sounds were used by Bird A at a higher rate than
others. In descending order, the greatest percentage of mimicked calls
over a year and calculated as a proportion of all vocalisations were
human (mean of 4%), then kookaburra (mean of 3.2%) , then peach
face (mean of 3%) and, rarely, budgerigars (0.5%). Over a three month
period, vocalisations consisted to 70% of species-specific vocalisations
whilst the remaining 30% were mimicked items. The practice of
mimicked human sounds accounted for a third (11% of total
vocalisations), 3% for peachface parrots and 2% for kookaburras. Bird
A also used segments of mimicked calls to make new sequences and to

integrate fragments of any mimicked calls into its own song. Dog barking was also found but significantly lower than that of these avian species caged nearby.   There were also variations in the amount of mimicry practice in response to hearing specific sounds for the first time. As Figure 2 shows, specific mimic segments received higher or lower amounts of practice when the stimulus changed (Fig. 2A) or was removed (Fig.2B).

In Figure 2A it can be seen that practice of kookaburra mimicry increased from near zero to over 3% in the month thereafter; in fact, two days after Bird A had been introduced into the adjoining cage. This level was maintained throughout the following month but declined during the two subsequent months. The first kookaburra call lasted less than a minute, yet two days later the magpie gave a complete rendering of that call (see also Fig. 3). Mimicry practice declined in the absence of any further calls. Then a second kookaburra joined the first, as silent as the first, and mimicry practice of the kookaburra sounds declined almost to zero. A month later, the two kookaburras joined for the first time for a duet. After this event, mimicry incorporation of kookaburra sounds increased steeply and remained high for several months thereafter. Interestingly, the practice after the first duet differed from the first mimicry in that the magpie attempted to copy the duet rather

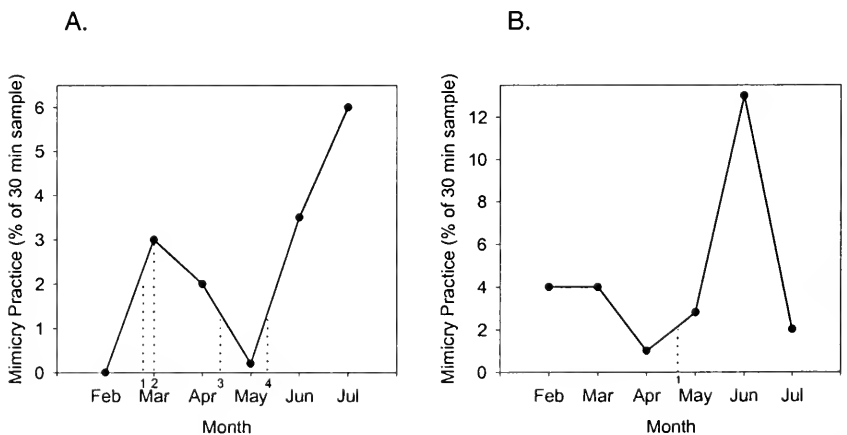A.   B.

Figure 2. Practice of mimicry by a magpie (referred to as bird A in text) of kookaburra and peachface parrots calls. Data are plotted as the percentage of time spent engaged in mimicry during a sample of 30 mins of all song vocalisations. A. Effect of additional Kookaburra calls on mimicry practice. The additions are shown with dotted lines: 1, First kookaburra call heard for the first time; 2, first instance of mimicry (two days later); 3, second kookaburra arrives; and 4, first duet between the two kookaburras occurs.   B. Effect of removal of Peachface parrots calls on mimicry practice. 1, time at which peachface parrots were removed from the outside aviary.

than the individual bird. Mimicry practice of the duetting rose to 6% two months later (Fig. 2A).

It seems significant that the practice of peachface parrot mimicry increased after the birds had been removed (Fig. 2B). Peachface parrots vocalise extensively and their removal to warmer winter quarters, along with the budgerigars, turned the aviary section into a relatively silent area. Instead of decreasing practice of the peachface parrots, Bird A in fact tripled the practice of their mimicry each day for almost an entire month, after which practice of peachface parrot mimicry declined to its earlier low level.

Figure 3 shows sound spectrograms of calls by kookaburras and their mimicry by a lyrebird and a magpie. Note that the magpie has attempted to copy the noise (blurred lines) in its rendering as well as the overtones of the sound rather faithfully: there are seven or eight harmonics in one sound (parallel lines) and the magpie's sound has the same number. Finally, the harmonics are not flat but curved downwards at each end and the magpie has copied this feature exactly. Note by comparison that the lyrebird's rendering is more rapid (8 syllables per 600 ms) than either that of the kookaburra or the magpie's copy. Lyrebirds, with their three syringeal muscles are more flexible. In the lyrebird's mimicry the structure of each harmonic is different, more like an open triangle (see arrow 4 in Fig. 3C) and the rendition is also not as loud as that of the original. Yet to the human ear, this lyrebird's mimicry of kookaburra call sounds very authentic.
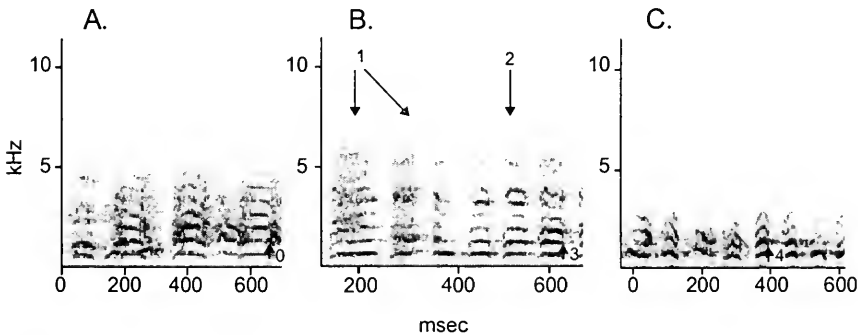

Figure 3. Comparison of mimicry by a magpie and a lyrebird. A, Sound spectrograms of a kookaburra call. B. Mimicry of the kookaburra by a magpie. C. Mimicry of the kookaburra by a lyrebird. Specific features of the call are shown by the arrows: Arrow 1, the magpie copies the noise in its rendering and Arrow 2, overtones of the sound. Arrow 0, the harmonics curve downwards at each end. Arrow 3, faithful copying of this feature by the magpie. Arrow 4, example of lyrebird harmonic.
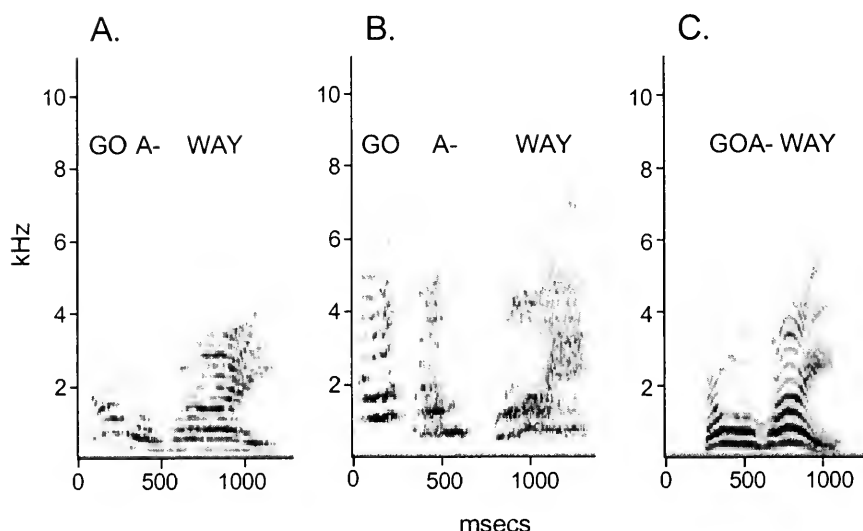
Figure 4. Mimicry of the human voice by a magpie. A. and C. Sonograms of two humans saying 'Go Away". B. Centre panel shows magpie mimicking this phrase.

Both lyrebirds and magpies have been known to mimic human speech. In Figure 4, an example is presented of a human speech segment that Bird A had learned and might have learned from either one or the other of the human voices presented in the sonograms of Figure 4. The human voice has many overtones (indicated by the layers of bars for each sound) and there are substantial variations from one human voice to another (Fig. 4A, C) . The magpie gave an audibly recognisable version of the phrase and attempted to use the complex overtone structure of each sound (see especially the syllable "go"). The phrase 'go away' was also clearly understood by people who had never heard a magpie speak. The magpie separated the 'a' from 'away' much more strongly than the human tutors. It is likely that this has to do with the bird's inability to use lips to form some consonants.

It is important to emphasise that the lyrebird's own territorial song is quite simple and substantially different from the sound structures of the calls that lyrebirds and magpies attempt to mimic (Fig. 5). The lyrebird's territorial calls usually have just one formant and few overtones. The magpie's own warble (quiet) song usually consists of a range of complex modulations but with just one formant and few overtones. The results have shown that in mimicry magpies copied rhythm, including pauses, overtones and modulations within each sound in such a way as to create the illusion of some other species vocalisation.
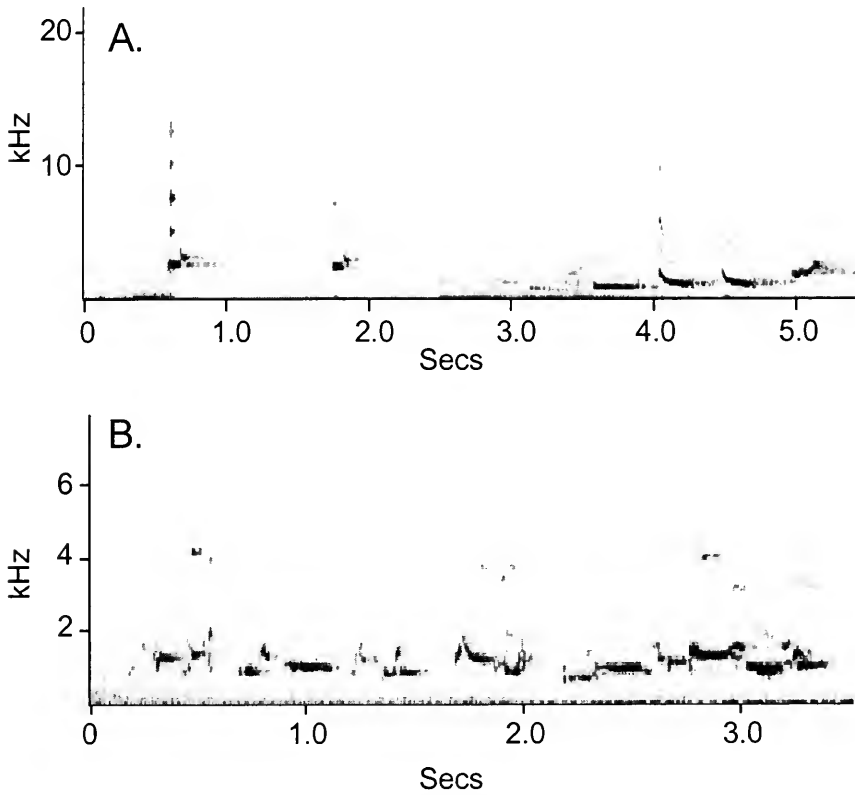
Figure 5. Sonograms of the species-specific song patterns of the A. superb lyrebird (territorial song) and B. the magpie (quiet warble). Pauses are rendered in true time.

The preciseness in the magpie's mimicry of other species was also demonstrated in a variation of mimicry of kookaburras by the magpie. Figure 6 shows the attempt by a magpie to copy not just the sounds of one kookaburra vocalisation but of the specific duets. Here we see that the magpie has accurately copied the two major formants, the flow of continuous sound and the pauses caused by one kookaburra briefly dropping out of the duet.

The study of examples of mimicry by wild magpies found evidence of mimicry of potential predators of young magpies (Fig. 1). One of them is the boobook owl (*Ninox novaeseelandiae*), an owl that is found throughout Australia. As this is only one isolated case, it is not clear whether this result is only a chance result or suggests a significant finding. Boobook owls are nocturnal and, on moonlit nights, magpies are crepuscular and even sing at times during the night. Hence there is opportunity for learning their call and for using it at a time when the
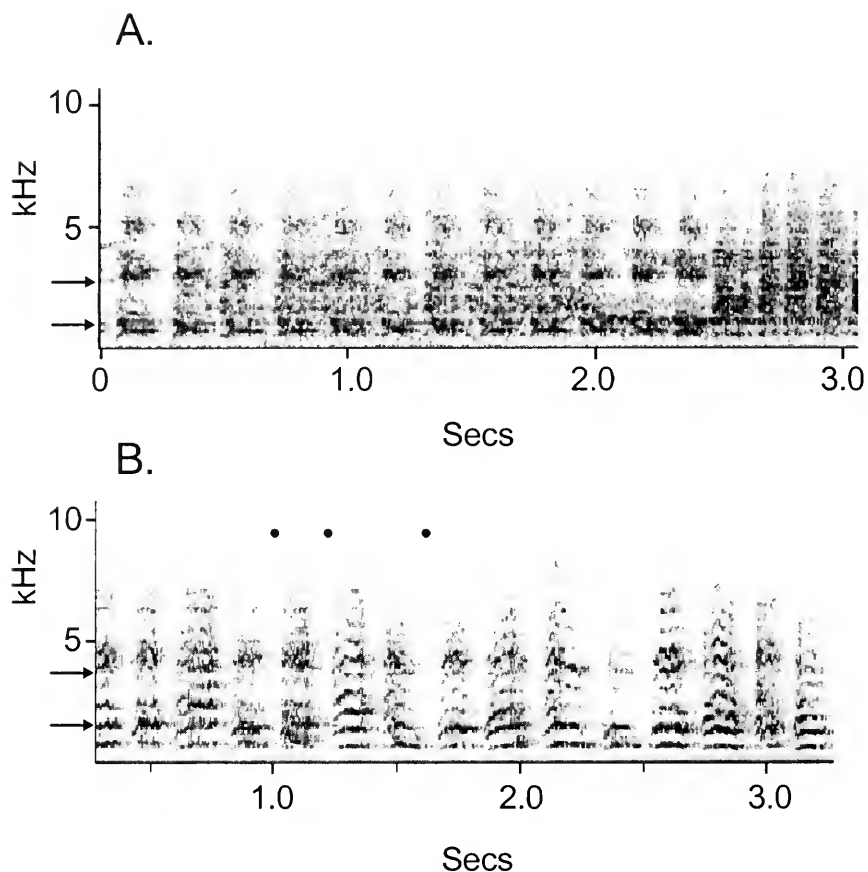
Figure 6. Mimicry of a kookaburra duet by a magpie. A. Sonograms of two captive kookaburras duetting. Only one bird was singing in the broad grey columns 1-3 and 10-12. B. Magpie mimicking the duet. The arrows indicate that the magpie has copied the two formants rather precisely. The dots above the columns show where it has also attempted to mimic the flow of continuous sound with lots of noise. The magpie also attempted to mimic the pauses caused by one kookaburra briefly dropping out of the duet.

owls are active. One isolated case of the mimicry of a barking owl (*Ninox connivens*) was also found amongst examples collected of wild magpies. This example was submitted to me as an example of mimicry of a dog barking. Analysis showed that it was not a dog but the owl. There may be more examples of barking owl mimicries that have so far been held to be dog barks. The sounds are easily confused but the sonogram reveals that the structure of a dog bark and the vocalisations of a barking owl are markedly different. The barking owl is a known threat to magpie young.

The study found that magpie mimicry is particularly accurate in

terms of the structure of the sounds that the bird mimics. Figures 1, 3, 4 and 6 show this astuteness very clearly. In particular, it is worth noting the differences of sound structure between those of an owl and a horse (Fig.1) and to assess Figure 3 again, showing the comparison of sound rendition between a real kookaburra, a magpie and a lyrebird. In terms of structure of sounds, the magpie's mimicry is far more accurate than that of the lyrebird. In other words, the lyrebird's mimicry is impressionistic while the magpie's is realistic. It is also important that the same captive bird that learned to mimic the captive kookaburra in close proximity also altered its mimicry of the kookaburra sounds once it had heard the duet of two kookaburras (Fig. 6). The same attention to details of sound structure are evident throughout all examples of mimicry that were collected of wild and captive magpies. The obvious degree of accuracy in rendering the main features of the structure of sound in the mimicry by magpies and the adaptation of that mimicry to new variations are the main findings of this study.

The vocal and auditory achievement of mimicking sounds becomes clear when these are compared to the species-specific vocalisations of either species, magpie and lyrebird. It is important to note that the structure of the lyrebird's song is relatively simple (see Fig. 5) and both species usually remain within a limited frequency range and a limited number of overtones. Both species show pure tones (single dark line) and melodious flow of song. The magpie song is generally more complex. Most vocalisations occur between 400 Hz and 6 kHz.

The results showed that mimicked sequences were incorporated (Fig. 7) in such a way that these incorporations, to some extent, seemed rule governed. Certain basic structures were found in all magpie samples of mimicry collected. For instance, there was not one single example of song closure on a mimicked sound. The bird always returned to one or two of its favourite closing phrases (species-specific) before closure. All mimicked sequences were embedded in one ongoing phrase that ended in closure either of its own individual identification phrase or in a specific three-tone trill (Fig. 7). As can be seen in the lower panel of Figure 7, the individual 'signature' is no more than two to three seconds long. Finally, phrases involving elements of mimicry in magpie song were highly variable. Figure 7 shows the incredible vocal versatility of the magpie's vocal abilities, ranging over four octaves and varying between soft segments, crescendos and strong finales. Note the rapid staccatos of the peachface parrot mimicry.

Unlike lyrebird breeding songs that are characterised by fixed patterns of sequence, the positioning and use of mimicry in magpie song appears to be arbitrary. Establishing the exact sequencing statistically is still a work in progress. There was no apparent regularity

in sequence of mimicked sounds. They seemed to be in random order. By contrast, lyrebirds appear to string mimicked sequences together in an unchanged order, referred to as the Albert cycle (Robinson & Curtis, 1996). Any additions are added on but then the bird eventually returns to the beginning of the sequence and starts all over again in the same order.
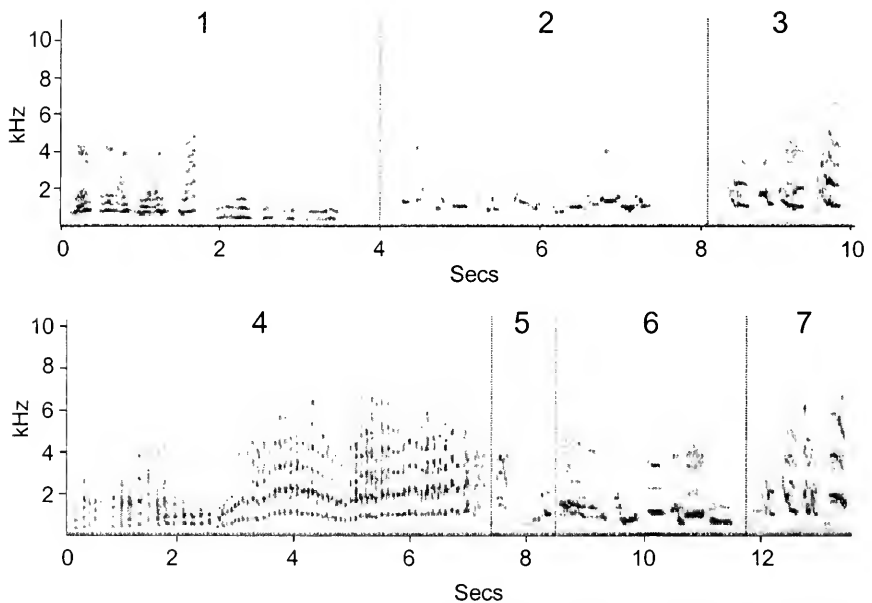

Figure 7. Integration of mimicry into the magpie's own song. The phrases are separated by dotted lines and are marked 1-7. They represent: 1, mimicry of human vowel sounds; 2, species-specific warble (typical song type of magpies); 3, closure of phrase by a four syllable magpie specific call type. Segments 4-7 represent another song; 4, shows the rapid staccato mimicry of peachface parrots; 5, a transition two-sylllable call that, in structure, is similar in amplitude and overtones and is a modified magpie alarm call; 6, is a call specific to this individual bird (an individual signature) and 7, indicates closure of the phrase. Note that in this second example, again, the phrase begins with a mimicked sequence, and it ends with a magpie-specific closing phrase (only two or three types of closing phrases were ever used by this individual bird and they never occurred elsewhere in the song).

DISCUSSION

The study is the first to establish that mimicry amongst Australian magpies is not confined to a specific region or subspecies. It occurs in magpies distributed widely across the Australian continent. Furthermore, the results reported here have shown that magpies do not mimic as an artifact of captivity, as many Australian parrot species appear to do, but mimicry patterns freely developed in wild birds. In fact, mimicry is widespread and highly developed amongst Australian bird species in general. The best known species for mimicry in the wild are lyrebirds (both species), Australian magpies and bowerbirds (several species). In contact with humans, even if remaining free, these species can also mimic human speech. Amongst European birds, the starling is the star of mimics (West & King, 1990; West, Stroud & King, 1983). In North America it is perhaps the northern mocking bird. We know that parrots and budgerigars are excellent mimics in captivity but the first examples of parrot mimicry in the wild have been found only recently and for one species only, the Grey parrot (Cruickshank, Gautier & Chappuis, 1993).

My research suggests that, in magpies, mimicry is performed both in solitude and in company, is independent of the breeding season and is voiced by males and females alike. By contrast, the mimicry of the lyrebird is confined to the breeding season and to the breeding song of the male only (Robinson & Curtis, 1996).

The data indicate adaptation and a substantial learning plasticity early in life. The mimicked sounds were not all learned at the same time but at different times throughout the observation period. David Attenborough claimed in his series 'The Life of Birds' (BBC, 1998, Episode 7) that the lyrebirds knew about 20 mimicked sounds. I have found no reference to substantiate this claim. However, if this is true, then the magpie and lyrebird may be very similar in mimicry repertoire size. The present study identified 15 types of mimicry of unambiguous sounds and there might have been more since rigid criteria had to be met before a sequence was considered to be mimicry.

Sampling of mimicry in lyrebirds in the wild is relatively accessible because the breeding song is part of a breeding display. The male clears a mound within the forest and dances. Time and place for the vocal performance are fixed and the amplitude of the song, carrying for several miles through the forest, make it relatively simple to locate the bird. Furthermore, many of the vocalisation recordings are taken from individual male birds that have habituated to human company (as for instance in Sherbrook Forest near Melbourne) and so allow very close proximity of humans during their courtship dance. By contrast,

magpie mimicry is sporadic and not tied to time of year or specific occasions.   For this reason, it has remained difficult to document. Using recordings obtained by people at many separate locations in Australia, and doing so by drawing on a vast audience of listeners to Australia's most popular radio science program, it has been possible to document mimicry in wild Australian magpies.

The question remains: What is the function of mimicry? Why would birds deliberately transgress their species-specific sounds and move into the vocal territory of other species? It has been postulated that mimicry may be no more than a mistake in copying species-specific song correctly (Catchpole & Slater, 1995).   This may be a possibility especially when closely related species (with somewhat different songs) hold nearby territories, but this option has to be ruled out for both the Australian magpie and for the lyrebird. At least in the case of the magpie, it was possible to show that mimicry practice is deliberate, selective and that the magpie responds to auditory stimuli external to its species. The very deliberate nature of the practice of certain mimicry types suggests that the mimicked type is intentionally learned and practised. A specific memory is established. The lyrebird renditions of mimicked sounds in specific sequences makes each mimicry type seem like a collector's item.   Presumably, the male lyrebird's search for embellishments could have derived from its own song.   However, as Figure 6 shows, the basic territorial song of the lyrebird is quite simple. While this song may be based on a genetically encoded template, the breeding song may have developed in response to sexual competition and it involves learning. The capacity to mimic in this species appears to have evolved over long periods of time.

Another hypothesis, that mimicry may result from selection for large song repertoires, has been in the literature for many years (see, for instance, Witchell, 1896).   Both magpies and lyrebirds have exceptionally large repertoires and it could be argued that more 'mistakes' are therefore possible. Kroodsma and Pickert (1984) argued that for large song repertoires it was either impossible or costly to encode genetically very specific controls over which songs are learnt. There will thus be an increased probability of interspecific mimicry associated with selection (by any mechanism) for large song repertoires (Kroodsma & Pickert, 1984).   There is some merit in this view. However, all this is ultimately saying is that basic qualities can be developed and enhanced through learning. The fact that both magpies and lyrebirds need to practise to retain the mimicked items should lead one to assess the mimicry in a positive rather than negative light- not as a mistake but as an acquired capability. Particularly the accuracy of the magpie's mimicked sounds ought to lead one to the conclusion that this

species has a very highly developed auditory perception and great musical discriminatory abilities.

Another hypothesis on mimicry deals with predation and mimicry. We know that insects may mimic appearance, smells and even light signals and dolphins and seals may use some vocal mimicry, but as far as is known to date, only birds mimic other species extensively in vocalisation. Purists argue that such mimicry by birds is not 'true' mimicry, 'true' mimicry being defined as having deceptive purposes useful for survival. Taking the models from studies of the insect world, 'true' mimicry involves three parties: the true identity of the mimicked one, say butterfly A, the mimicker called butterfly B, and the predator which is fooled by butterfly B (i.e., will not eat it because it looks like the unpalatable butterfly A). It is not clear why this model of mimicry should be binding for avian species. However, the literature still grapples with these issues and for good reason (Veerman, 1994). It is possible to conceive that a limited amount of the mimicry found in magpies might support the view that some avian mimicry is for the purpose of dealing with predators. Indeed, Robinson argued that mimicry was most likely to emerge in species exposed to predation (Robinson, 1975).

There has been no unambiguous evidence to date that birds mimic to avoid predation. However, it is possible that birds may mimic another to safeguard a territory. While this is not predation, such mimicry would also have clear survival function either in safeguarding a territory from a predator using a similar food chain as the species defending its territory, or by repelling a predator who may consider preying on the young in the nest. I have found evidence, only one recording respectively, of a wild magpie mimicking potential predators of their young, such as the barking owl and the boobook owl. Martine Hausberger, however, has noticed that starlings mimic predators in vain (personal communication, Rennes, July 2000). Apparently, the predators took no notice at all of the mimicry (see also Hausberger, Jenkins & Keene, 1991). The discovery that the Australian magpie also imitates two of potential predators of their young, the barking owl and the boobook owl, may add some credence to the view that mimicry may serve a function against predators, although it is not very strong evidence to date.

Some species mimic the calls of species that prey on them in order to teach their own young about the dangers. This has been noted in many species of the African Turdinae; when potential predators come close to their young, adults intersperse their own calls with mimicked calls of the predator (Oatley, 1971). The young may thereby learn the calls of the predator and so learn to avoid that species, although in this

case the mimicry may be used to drive off the predator rather than being a way of teaching the young to recognise the predator. There is no recorded evidence that Australian magpies incorporate mimicry in order to teach their offspring to recognise predators. However, in my research on vocal development of magpies at different nest-sites and throughout the dependent fledgling period, I observed that feeding parents sing to their offspring just before they feed. These observations were made on seven independent occasions. Parent and sibling were standing on the ground and, before the parent handed over the food to the offspring, it would sing a short phrase. Another example of this practice was found on the tapes of Carrick, Robinson and Falls (1965). This provided the only recorded example found of this practice involving mimicry. The female landed on the nest and mimicked the neighing of a horse before she fed the nestlings.

A third reason for mimicry, and the one most commonly cited, is related to the breeding season. Earlier studies on lyrebirds argue that mimicry is used purely as embellishment to increase chances of mating (Thoburn, 1978). Male lyrebirds certainly adorn their songs during breeding season with all manner of sounds, taken from the sound repertoire available to the male. This typically includes mimicry of other birds, the most distinctive ones being currawongs, kookaburras, yellow tailed black cockatoos and catbirds (mostly species which mimic others themselves). Sounds they include may also be barking dogs, car horns, creaking door hinges, car horns and even chain saws and many other animate and inanimate objects, all sound segments with which the bird will then liberally spice its own species-specific calls. It appears that lyrebirds sing their long sequences of mimicked calls to attract the female. It is as if they 'wear' the song component like trophies - the more elaborate and the more frequent the mimicry, the more the female may be impressed. Displays to outdo competition are common amongst polygamous and promiscuous males of class Aves. These vocalisations contain extremely beautiful musical sequences that are strung together to make a statement and attract a female (Robinson & Curtis, 1996).

Although this view of mimicry (embellishment) may explain the function of mimicry in the breeding song of the lyrebird it is not applicable to the Australian magpie since males do not sing solely to attract females. Further, phrases involving elements of mimicry in magpie song are highly variable. Unlike lyrebird breeding songs that are characterised by fixed patterns of sequence, the positioning and use of mimicry in magpie song appears to be arbitrary or, at least, highly complex.

Magpie song appears not to be organised sequentially. Magpie

mimicry is an integral part of song but, as the results have shown, the mimicked sounds are not random. Bird A might have mimicked visiting butcherbirds, occasional horses, cars, car horns, sirens, visiting cats and sounds of migratory birds. However, Bird A never utilised any of these sound sources. The only mimicked sounds stemmed from other long term aviary companions nearby and from constant sound companions of the captive magpie. These were budgerigars, peachface parrots (both species captive), kookaburras (rehabilitating), the dogs belonging to the property and humans (Table 1). To give an example. A juvenile butcherbird visited the aviary daily for a week, vocalising almost continuously. The rehabilitating magpie often joined in and sang a kind of duet with the butcherbird. Both in terms of purity of sound and in vocal range, the sounds of the grey butcherbird would be easily manageable for the magpie. However, Bird A never mimicked the butcherbird. By contrast, the convalescing kookaburra, too ill to vocalise much, vocalised only three times between April and June of 1996. Each of the vocalisations lasted less than a minute. The magpie mimicked the vocalisation after first exposure (of only less than a minute). A day after the 'laughing' sound of the kookaburra was first emitted, the magpie already fully incorporated this sequence into its own song. Moreover, as Figure 2 showed, the addition of a second kookaburra a little later and the first ensuing mimicry of that duet, increased practice of this mimicry which was retained for months thereafter.

The fact that the magpies included in this study seemed to mimic only sounds that were relevant and within their own territory suggests something about vocal learning in sedentary species. It is perhaps not so much a matter of the size of the repertoire as was argued before, but of social organisation (although the two are also often interlinked). A bird with a complex social organisation, as has the magpie, may require a map of its territory that is recorded not only visually but in an auditory fashion. This study found that mimicry in *Gymnorhina tibicen* is used exclusively for sound features belonging to inhabitants in the bird's own territory, as distinct from visitors to that territory.

ACKNOWLEDGEMENTS

mimicking a boobook owl. Sincere thanks go to Edric Slater, formerly of the CSIRO, for his expert advice. From him I also received a sound recording of a talking Musk Duck and of a talking lyrebird. From Syd Curtis I received papers and recordings of lyrebirds. Dr. Peter Fullagar, CSIRO Wildlife Sound Archives in Canberra, was chief in helping me identify magpie mimicry of certain bird species. A warm thank you also to Prof. Bruce Falls of Toronto, Canada, who worked with Prof. John Carrick on Australian magpies in Canberra in the 1960s, for generously making his original study tapes available and to the many members of the public who willing helped with information and supplied tapes for this study and to Robyn Williams of the Science Show, ABC, to allow me to broadcast my wish to get samples of magpie mimicry on national radio. This paper is part of my research for a second PhD. My sincere thanks to Prof. Judith Blackshaw for her ongoing support and to Prof. Lesley Rogers for making many helpful suggestions in the process of collecting and analysing data.

REFERENCES

Baker, A., Mather, P., & Hughes, J. (1995). *The estimation of dispersal and gene flow in populations of the Australian magpie.* Paper presented at the Australian Society for the Study of Animal Behaviour, 22nd Annual Conference, 20-22 April, Brisbane.

Brown, E. D., & Farabaugh, S. M. (1991). Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*, III: Sex Specificity and individual specificity of vocal parts in communal chorus and duet songs. *Behaviour, 118* (3-4), 244-274.

Brown, E. D., Farabaugh, S. M., & Veltman, C. J. (1988). Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*, I. Vocal sharing within and amongst social groups. *Behaviour, 104*(1-2), 1-28.

Burton, T. C., & Martin, A. A. (1976). Analysis of hybridization between Black-backed and White-backed Magpies in south-eastern Australia. *Emu, 76*, 30-36.

Carrick, R. (1963). Ecological significance of territories in the Australian Magpie. *Proceedings of the International Ornithological Congress, 13*, 740-753.

Carrick, R. (1972). Population ecology of the Australian black-backed magpie, royal penguin and silver gull. *Population Ecology of Migratory Birds: A symposium, U.S. Department of the Interior, Wildlife Research Report, 2*, 41-99.

Catchpole, C. K., & Slater, P. J. B. (1995). *Bird Song. Biological Themes and Variations.* Cambridge: Cambridge University Press.

Chisholm, A. H. (1948). *Bird Wonders of Australia.* Sydney: Angus and Robertson.

Clunie, F., & Morse, P. (1984). *Birds of the Fiji Bush.* Suva: Fiji Museum.

Cockburn, A. (1996). Why do so many Australian birds cooperate: social evolution in the Corvidae. In R. B. Floyd, A. W. Sheppard, & P. J. d. Barro (Eds.), *Frontiers in Population Ecology* (pp. 451-472). Melbourne: CSIRO.

Cruickshank, A. J., Gautier, J.-P., & Chappuis, C. (1993). Vocal mimicry in wild African Grey Parrots *Psittacus erithacus. Ibis, 135*, 293-299.

Farabaugh, S. (1982). The ecological and social significance of duetting. In

D.E.Kroodsma & E.H.Miller (Eds.), *Acoustic Communication in Birds* (Vol. 2, pp. 85-124). New York: Academic Press.

Farabaugh, S. M., Brown, E. D., & Hughes, J. M. (1992). Cooperative territorial defence in the Australian magpie, Gymnorhina tibicen (Passeriformes, Cracticidae), a group-living songbird. *Ethology*, *92*(4), 283-292.

Farabaugh, S. M., Brown, E. D., & Veltman, C. J. (1988). Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*, II. Vocal sharing between territorial neighbours, within and between geographic regions, and between sexes. *Behaviour*, *104*(1-2), 105-125.

Gramza, A. F. (1972). Avian Vocal Mimicry: The Phenomenon and its Analysis. *Zeitschrift für Tierpsychologie*, *30*, 259-265.

Hausberger, M., Jenkins, P. F., & Keene, J. (1991). Species-specifity and mimicry in bird song: Are they paradoxes? A reevaluation of song mimicry in the European starling. *Behaviour*, *117*, 53-81.

Kaplan, G. (1998). Vocal Mimicry and territoriality in the Australian Magpie *Gymnorhina tibicen*. Ostrich. *Journal of African Ornithology*, *69*, 256.

Kroodsma, D. E., & Pickert, R. (1984). Repertoire size, auditory templates, and selective vocal learning in songbirds. *Animal Behaviour*, *32*, 395-399.

McIlroy, J. C. (1968). *Biology of Magpies (Gymnorhina sp.) in New Zealand.* Unpublished Masters, Lincoln College, Christchurch, New Zealand.

O'Neill, M. G., & Taylor, R. J. (1984). Co-operative hunting by Pied Currawongs *Strepera graculina*. *Corella*, *8*, 95-96.

Powys, V. (1995). Regional variation in the territorial songs of superb lyrebirds in the central tablelands of New South Wales. *Emu*, *95* (Part 4), 280-289.

Queensland National Parks and Wildlife Society.(1987) Magpie nesting. *Wildlife Information BP3 17*, 1.

Readers Digest. (1976). *Complete Book of Australian Birds*. Sydney: Reader's Digest Services.

Robinson, A. (1956). The annual reproductive cycle of the magpie, *Gymnorhina dorsalis* Campbell, in south-western Australia. *Emu*, *56*, 233-336.

Robinson, F. N. (1975). Vocal mimicry and the evolution of birdsong. *Emu*, *75*, 23-27.

Robinson, F. N., & Curtis, H. S. (1996). The Vocal Displays of the Lyrebirds (Menuridae). *Emu*, *96*, 258-275.

Sanderson, K., & Crouche, H. (1993). Vocal Repertoire of the Australian Magpie *Gymnorhina tibicen* in South Australia. *Australian Bird Watcher*, *15*(4), 162-164.

Schodde, R., & Mason, I. J. (1999). *The Directory of Australian Birds. Passerines.* Melbourne Collingwood: CSIRO Publishing.

Sibley, C. G., & Ahlquist, J. E. (1985). The phylogeny and classification of the Australo-Papuan passerine birds. *Emu*, *85*, 1-14.

Thoburn, L. (1978). *The vocal mimicry of the superb lyrebird.* Unpublished Honours Thesis, University of Sydney, Sydney.

Thorpe, W. H. (1961). *Bird song. The Biology of Vocal Communication and Expression in Birds*. Cambridge: Cambridge University Press.

Veerman, P. A. (1994). Batesian Acoustic Mimicry by the Regent Honeyeater. *Bird Watcher*, *15*(6).

Veltman, C. J. (1984). *The social system and reproduction in a New Zealand magpie population, and a test of the cooperative breeding hypothesis.* Unpublished Ph.D., Massey University, Palmerston North, NZ.

West, M. J., & King, A. P. (1990). Mozart's Starling. *American Scientist*, *78*(March-April), 106-113.

West, M. J., Stroud, A. N., & King, A. P. (1983). Mimicry of the human voice by European starlings: The role of social interaction. *Wilson Bulletin*, *95*, 640-643.

Witchell, C. A. (1896). *The Evolution of Bird Song*. London: Adam & Charles Black.

FAILURE TO FIND PROBOSCIS CONDITIONING IN ONE-DAY OLD AFRICANIZED HONEY BEES (*APIS MELLIFERA L.*) AND IN ADULT URUÇU HONEY BEES (*MELIPONA SCUTELLARIS*)

Charles I. Abramson
Oklahoma State University, USA

Italo S. Aquino
Universidade Federal da Paraiba, BRAZIL

Sherril M. Stone
Oklahoma State University, USA

ABSTRACT: The proboscis extension reflex was used to investigate behavior modification in one day old Africanized honey bees and in adult Uruçu honey bees. Experiments were designed to investigate classical conditioning, pseudoconditioning, and central excitatory state. Additional experiments examined the suitability of the proboscis extension reflex to serve as a feeding assay were carried out on Uruçu. The results indicated no classical conditioning and no pseudoconditioning in young Africanized bees or in the adult Uruçu. A large central excitatory effect was observed in young Africanized bees, but only a small effect was observed in Uruçu. The proboscis extension reflex could be used as an assay to test the suitability of artificial diets in Uruçu.

The study of the proboscis extension reflex (PER) has led to many areas of fruitful research in the honey bee (Kartzev, 1996; Menzel & Bitterman, 1983), including studies of Pavlovian conditioning (Bitterman, Menzel, Fietz, & Schäfer, 1983; Buckbee & Abramson, 1997; Menzel, 1987), discriminative punishment (Smith, Abramson, & Tobin, 1991); influence of pesticides on behavior (Mamood & Waller, 1990; Stone, Abramson, & Price, 1997; Taylor, Waller, & Crowder, 1987) olfactory discrimination (Getz & Smith, 1987; Smith & Menzel,

1989), and as a rapid bioassay to measure detection of adulterated beeswax (Aquino, Abramson, & Payton, 1999). Additionally, the PER has served as a model system for studying the biochemistry of learning and other forms of behavior modification in honey bees and other insects (Abramson, 1994; Menzel, Hammer, Braun, Mauelshagen, & Sugawa, 1991; Mercer, 1987).

Most recently, work on the PER has been directed toward the study of Africanized honey bees. Work with the so called "Killer bee" revealed the existence of a number of classical conditioning phenomena in adults, although the asymptotic level of performance is less than that observed with the European honey bee (Abramson, Aquino, Silva, & Price, 1997). The PER has also been used to study the influence of pesticides on learning (Abramson Aquino, Ramalho, & Price, 1999) and to measure attraction to consumer products such as soft drinks and perfumes in the Africanized honey bee (Abramson, Aquino, Azeredo, Filho, & Price, 1997).

The experiments reported here are designed to study behavior modification in the day-old Africanized honey bee. Invertebrates such as the fruit fly (*Drosophilia melanogaster*) and the mollusc *(Aplysia californica)* have been used as model systems to study gerontology and developmental issues in behavior modification but there is little comparative research with honey bees (Carew, Marcus, Nolen, Rankin, & Stopfer, 1990; Bhagavan, Benatar, Cobey, & Smith, 1994; Le Bourg, 1996). The rationale behind the experiments reported here are two-fold. First, the comparative analysis of learning in the Africanized honey bee would be incomplete if confined to the study of adults. Second, we had interest in providing some data on the ability of young bees to learn a PER Pavlovian conditioning task.

During the course of the experiments with Africanized bees we had the unique opportunity to work with the stingless honey bee, Uruçu. The question naturally arose whether the PER technique, so successful with both the Africanized and European honey bees, could be adopted to the study of Uruçu. The PER is most readily studied in Africanized and European honey bee by confining them in small metal harnesses. Once harnessed, bees readily extend their mouthparts (proboscises) to feed on a sucrose solution after the solution has been briefly applied to the antennae, on which sucrose sensitive contact sensillae are found. One potential difficulty is whether Uruçu will remain viable when restrained. A second potential problem is that, once restrained, will normal feeding behavior be possible. The ability to feed regularly when restrained is a necessary condition in PER research on learning.

A successful application of PER methodology to Uruçu is important not only for what it may reveal about the learning process in

this interesting honey bee but takes on an added significance because of the dramatic decline in the numbers of Uruçu in the northeast of Brazil. A major factor in this decline is the destruction of their natural habitats, food sources, and colonies by humans raiding hives for honey (Lorenzon, 1996). The honey is produced in such small quantities (about 1 liter per hive each year) it is extremely expensive at almost $100.00 a liter and therefore profitable to sell.

The Uruçu bee is slightly larger than the Africanized bee. It has an orange hairy thorax and orange tint to the antennae. In addition, it produces a very thin honey the color of which range from light green to dark yellow. The hives of Uruçu are smaller than *Apis* and consist of only a few hundred bees. They store their honey in honey pots and not in the familiar hexagonal cells so characteristic of *Apis*. Because Uruçu is a member of the family of stingless bees their defensive mechanisms are restricted to strong mandibles, small hive entrance, sticky entrance tunnels and honey, wax, and propolis that smell like unwashed socks.

GENERAL METHODS

Three series of experiments are common to both the Africanized honey bee and the Uruçu honey bee. In the first series, Pavlovian conditioning of proboscis extension is examined. An investigation of pseudoconditioning is the purpose of the second series of experiments. In the third series, the influence of central excitatory state is researched. In addition to Pavlovian conditioning, pseudoconditioning, and central excitatory state, the usefulness of the PER technique as a feeding assay was examined in Uruçu. All Africanized and stingless bees were obtained from, and ˙studied in, the Laboratório Apícola of the Universidade Federal da Paraiba (UFPB), Bananeiras, Brazil.

Subjects

One day old Africanized honey bees (Apis mellifera L.). Frames containing brood were brought to the laboratory at 9:00 AM on the day prior to the experiment and placed in an observation hive. The use of the observation hive assured us of the age of the bees and, as an added advantage, made them easier to capture. Within 15 seconds of emergence Africanized worker honey bees (*Apis mellifera L.*) were captured and harnessed in small metal tubes. The young bees were placed in the harness without rendering them unconscious as was done with adult Africanized bees. We did not want to render newly emerged bees unconscious because we did not know what effect it would have

on the learning process. To secure the bee in the harness, a strip of duct tape was placed between the head and the thorax and fastened to the sides of the metal tube. Following harnessing, subjects were fed a 2.9 M sucrose solution to satiation and held overnight until testing at 12:00 PM the following day. The purpose of feeding was to equate motivational levels for the experiment that was to be run the following afternoon. Different sets of subjects were used for all the experiments described.

Adult Africanized honey bees (Apis mellifera L.). Adult workers (estimated to be 21 days old) were selected at random as they departed from the laboratory hive around 9:00 AM on the day prior to use and tested around 12:00 PM the following afternoon. Subjects collected in this way are a mixture of bees of different behavioral specializations that require either departure from the hive (e.g., foragers or nest cleaning bees) or remaining near the entrance (e.g., guards). Each bee was carried in a glass vial to the laboratory. Individual subjects were rendered unconscious by placing the glass vials in an ice water bath. When the bee became inactive it was immediately removed from the vial and put into a metal restraining harness. After regaining consciousness, subjects were fed a 2.9 M sucrose solution until its proboscis would no longer remain in contact with the solution, after which they were left until trained the next morning (for details see Abramson, Aquino, Silva, *et al.*, 1997). The rationale behind the prefeeding was to ensure that all subjects had the same motivation to feed.

Stingless honey bees (Melipona scutellaris). Adult worker Uruçu bees (estimated to be 15-20 days old) were selected at random from the laboratory hive around 9:00 AM on the day prior to use and tested around 12:00 PM the following afternoon. Subjects were placed in the same harness used for the Africanized bees. As with the young Africanized honey bees, the Uruçu were placed in the harness without rendering them unconscious. After being placed in the harness subjects were fed Uruçu honey. Subjects were fed honey, until satiated, and not the sucrose solution used for the Africanized bees because the sucrose solution would not elicit proboscis extension. Different sets of subjects were used for all of the experiments described.

Apparatus

Materials consisted of the metal harnessing tubes (0.6 cm inside diameter and 2 cm long), a ventilation chamber to prevent the accumulation of the conditioned stimulus (CS) and unconditioned

stimulus (US) scents in the testing area, plastic 20 cc syringes to present the CS and filter paper strips (handled with tweezers) to administer the US or a distilled water CS. Three classes of CSs were used: 1) oils (obtained from Sigma Chemical Company, St. Louis, MO), 2) wax (Africanized and *Melipona*), and 3) water stimulation to an antennae.

Geraniol (Sigma Chemical product number G-5135), Citral (Sigma Chemical product number C-1645), and Hexanal (Sigma Chemical product number H-9008) constituted the oils. The oils and water were applied neat onto a piece of 1-cm^2 filter paper strips (Whatman #1).

The filter paper containing the oils was secured to the plunger of the syringe (one syringe for each oil used) with a metal thumbtack. The filter paper containing water was simply held with tweezers. The wax (AHB wax - 3.3 grams, *Melipona* - 1.9 grams) were obtained from the laboratory hives and placed into a syringe were it remained for 3 days prior to use. The conditioned stimulus was the odour of bees wax or oils and was selected based on their effectiveness shown in our previous research (Abramson, Aquino, Silva, *et al.*, 1997). To administer an olfactory CS, the syringe is depressed near the head of the subject. Following a trial the plunger of the syringe is pulled back in preparation for the next CS presentation. To administer antennae stimulation of the CS, the filter paper was dipped in distilled water and held between the jaws of a tweezer. It was then briefly applied to an antennae (the use of the left or right antennae was counterbalanced between subjects). The rationale behind the use of several CSs was not to restrict our findings to a particular CS. For young and adult Africanized honey bees the US consisted of a 2.9 M sucrose solution. Because the Uruçu bees did not respond to the sucrose solution used for the Africanized bees, Uruçu honey served as the US for the stingless bees. The honey was obtained directly from the Uruçu colony.

SERIES 1: PAVLOVIAN CONDITIONING STUDIES

In the first series of experiments we investigated Pavlovian conditioning in day old Africanized honey bees and adult stingless bees. To our knowledge no such studies have been attempted with these two species of honey bees.

Procedure

Africanized bees. One hundred and twenty young bees (one day old) were randomly assigned to one of 6 groups (20 subjects per group). The groups differed primarily in terms of the CS used (Hexanal, Africanized honey bee wax, and water stimulation of the antennae) and

whether they received paired or unpaired training. In addition to the one day old bees, forty adult Africanized bees were also used and randomly assigned to one of two groups (20 subjects per group). For the adult groups, Hexanal and wax served as the CS, respectively. The adult groups were included to ensure that learning could occur during the time of year these experiments were conducted (July/August 1998). Unpaired controls were not run for the adult groups because the results of several experiments (using both paired and unpaired comparisons and discrimination procedures) rendered them unnecessary (Abramson, Aquino, Silva, *et al.*, 1997; Abramson *et al.*, 1999).

For all paired groups there were 12 acquisition trials followed by 12 extinction trials. If no learning was evident, extinction trials were not conducted. During acquisition a non-overlap procedure was used in which the CS terminated before the US was presented. Upon termination of the CS, the US was presented by first touching sucrose to the antenna and then to the now extended proboscis. The CS duration was 3 seconds and the US was a 2 second feeding of a 2.9 M sucrose solution. The intertrial interval was 10 minutes for paired animals and 5 minutes for unpaired. The unpaired groups were included to ensure that any increase in the probability of proboscis extension to the CS was the result of CS-US pairings and not a nonassociative effect such as sensitization.

Unpaired CS/US stimuli were presented in pseudorandom order. For half the unpaired animals, stimulus presentations consisted of three successive sequences of CS US US CS US CS CS US. For the remaining animals the sequence consisted of US CS CS US CS US US CS. The interval between stimulus presentations was five minutes - half the time for paired animals. The rationale behind using a five minute intertrial interval for unpaired animals was to keep the time between CSs presentations approximately 10 minutes. If a 10 minute intertrial interval was used then the time between CS presentations would be approximately 20 minutes and any difference between paired and unpaired animals might be accounted for in terms of such nonassociative effects as time spent in the apparatus.

Conditioned responses to the CS were categorized visually into one of two states during each trial. If a subject extended its proboscis after the onset of the CS, but before its antennae were touched with the sucrose, a response was registered. Otherwise, a non-response was recorded.

Stingless bees. Two hundred and forty adult Uruçu honey bees were randomly assigned to one of 12 groups (20 subjects per group). As in the Africanized bee experiments the groups differed primarily in

terms of the CS used and whether they received paired or unpaired training. The major difference between the Africanized bee experiment and the Uruçu experiment is that a greater range of CSs were used (Hexanal, Geraniol, Citral, Uruçu wax, Africanized honey bee wax, and water stimulation to the antennae). Geraniol, Citral, and Uruçu wax were included because we wanted to test a range of CSs as was done in our original work with Africanized bees (Abramson, Aquino, Silva, *et al.*, 1997). In addition to using a greater variety of CSs, the second difference between the Africanized and Uruçu experiments was the use of Uruçu honey as a US. The change was necessary because the Uruçu did not drink the sucrose solution so effective with Africanized bees. With the exceptions already noted, all training variables and the use of unpaired control groups were identical to those used in the Africanized experiments.

RESULTS AND DISCUSSION

Figure 1 shows the mean proportion of animals responding to paired presentations of a Hexanal, AHB wax, or antennae stimulation CS with a sucrose US in one-day old Africanized honey bees. To insure that conditioning can occur during the time these experiments were run, the results of two adult Africanized honey bees groups are also presented. The adult animals showed a learning curve typical of our previous studies of Pavlovian conditioning in Africanized honey bees. In contrast, the one-day old honey bees showed no evidence of learning despite responding to the sucrose US on each training trial. As would be expected from these data, performance of unpaired animals did not differ from paired animals. Figure 2 presents the results of the 3 unpaired groups. As in the paired groups there is little responding to the CS and all one-day old honey bees responded to each presentation of the US.

As would be expected from the figures, the results of the repeated measures ANOVA for the adult AHB indicates a significant Group effect $F(1, 38) = 4.753$, $p = .036$, a Trial effect $F(11, 418) = 10.603$, $p = .000$, and a non-significant Group x Trial interaction $F(11, 418) = .240$, $p = .995$. A similar analysis conducted on the data for the three paired one-day old AHB indicates no significant Group effect $F(2, 114) = 2.544$, $p = .087$, no Trial effect $F(11, 627) = 1.772$, $p = .055$, and no Group x Trial interaction $F(22, 627) = .641$, $p = .896$. Overall comparisons between one-day old paired and unpaired groups reveal no significant Group differences $F(1, 114) = 2.232$, $p = .138$.
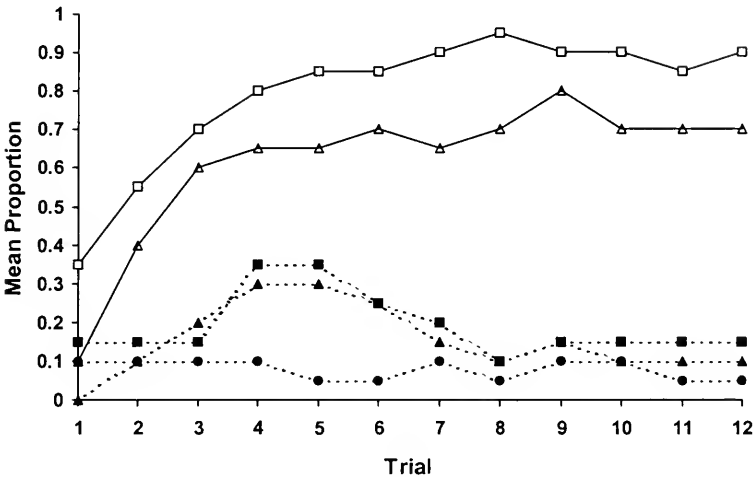
Figure 1. Mean proportion of adult and one day old Africanized honey bees responding to a CS over the course of 12 acquisition trials. Performance is shown in AHBs for both adults (unfilled symbols) and day olds (filled symbols). Different CSs were used as follows: Beeswax (squares); hexanal (triangles); and antennae stimulation (circles). No conditioning is evident in day old bees.
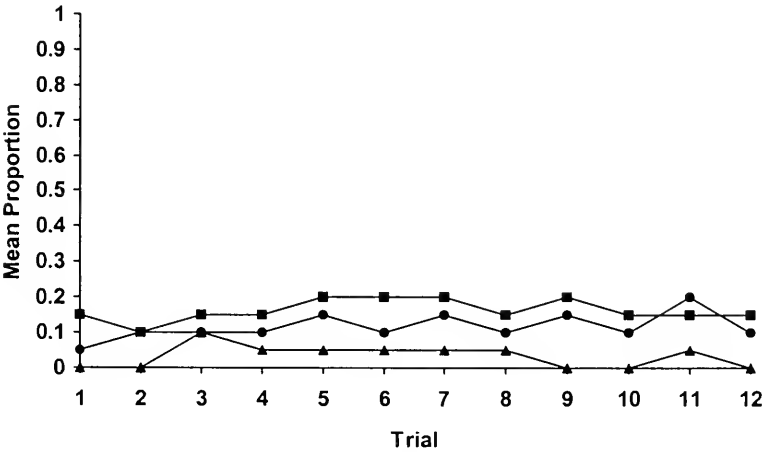

Figure 2. Mean proportion of one day old Africanized honey bees responding to a CS which was explicitly unpaired with a US. Performance using different CSs is represented as follows: Beeswax (squares); hexanal (circles); and antennae stimulation (triangles).

In Figure 3 the data are again plotted to show the comparison between adults and one-day old AHBs when beeswax and hexanal served as the CSs. Both wax and hexanal were readily associated with the US in adults but not in day old bees. We find this result interesting because both adults and young bees responded to each presentation of the US although none acquired an association with the CS. The differences between adults and young bees are supported by the results of a repeated measures ANOVA which indicated a significant Group effect $F(1, 76) = 112.191$, $p = .000$, a Trial effect $F(11, 836) = 7.950$, $p = .000$, and a Group x Trial interaction $F(11, 836) = 5.029$, $p = .000$.

Figure 4 shows the mean proportion of Uruçu honey bees responding to paired presentations of Hexanal, Geraniol, Citral, Uruçu wax, AHB wax, or antenna stimulation. No conditioning is evident in any of the groups despite each animal responding to the US. The results of the repeated measures ANOVA for the adult Uruçu indicated no significant Group effect $F(1, 38) = 2.652$, $p = .112$, no Trial effect $F(11, 418) = .918$, $p = .523$, and no Group x Trial interaction $F(11, 418) = 1.541$, $p = .114$.
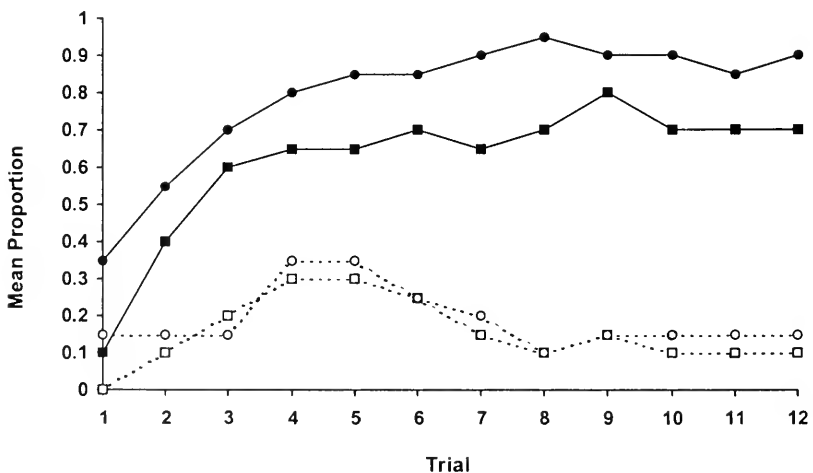
Figure 3. Mean proportion of adult (filled symbols) and one day old Africanized honey bees (open symbols) responding to a CS of either beeswax (circles) or hexanal (squares) during paired training.
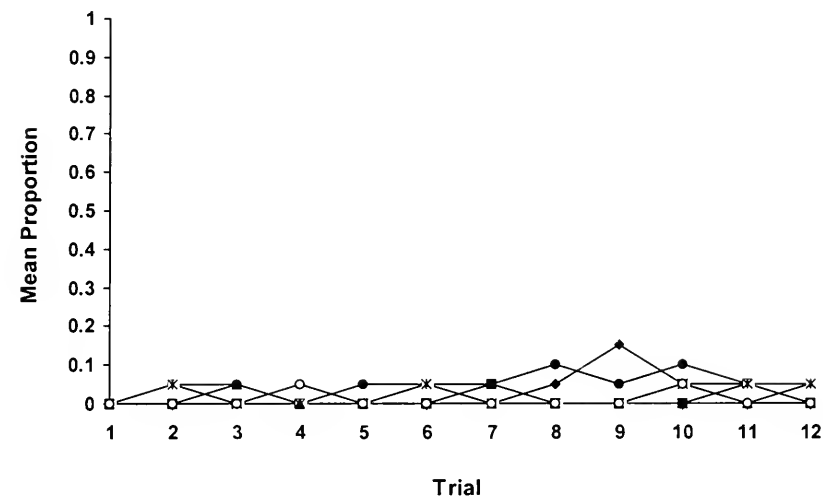
Figure 4. Mean proportion of adult Uruçu honey bees responding to different CS's over the course of 12 acquisition trials. Performance using six different CS's is represented as follows: AHB wax (filled squares); antennae stimulation (filled circles); geraniol (filled triangles); hexanal (filled diamonds); Uruçu wax (stars); and citral (unfilled circles).
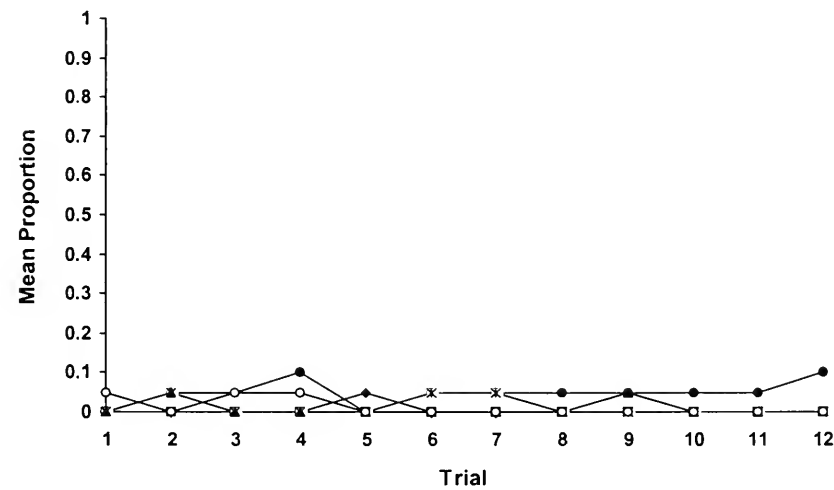

Figure 5. Mean proportion of adult Uruçu honey bees responding to a CS which was explicitly unpaired with a US. Performance is shown for six different CS's as follows: AHB wax (filled squares); antennae stimulation (filled circles); geraniol (filled triangles); hexanal (filled diamonds); Uruçu wax (stars); and citral (open circles).

Figure 5 presents the results of the six unpaired Uruçu groups. As is the case of one-day old bees and the adult Uruçu, few Uruçu respond to the CS when the CS and US are explicitly unpaired. Overall comparisons between adult paired and unpaired Uruçu revealed no significant Group differences $F(1, 228) = .691$, $p = .407$. It should be noted that the original design of the one-day old AHBs and Uruçu experiments included 12 CS-only extinction trials. Because no acquisition was obtained in the one-day old AHBs nor in the Uruçu bees, extinction trials were not necessary.

SERIES 2: PSEUDOCONDITIONING STUDIES

In the previous series we found no evidence for Pavlovian conditioning in day old Africanized honey bees nor in adult Uruçu. The present series of experiments looks for another type of behavior modification known as pseudoconditioning.

Pseudoconditioning refers to any "conditioning" that is not shown to have been dependent upon the correlation between the CS and US (Grether, 1938; Harris, 1943). It is most readily studied by exposing animals to a series of US presentations followed by a CS only test trial. If the animal responds to the CS even though the CS was not explicitly paired with the US, pseudoconditioning is indicated. Traditional controls for pseudoconditioning include explicitly unpaired CS/US presentations and discrimination training. Two explanations have been offered to account for pseudoconditioned responses. One explanation suggests that the unconditioned response generalizes to stimuli resembling the unconditioned stimuli. The alternative explanation suggests that exposure to an unconditioned stimulus produces a change within the organism that would cause the organism to respond to any external stimulus (Mackintosh, 1974).

Pseudoconditioning is readily observed in invertebrates including polychaete worms (Evans, 1966a, b) and octopuses (Young, 1960) and is considered a major form of behavior modification in invertebrates (Well, 1968). A study of olfactory conditioning in the earthworm revealed substantial amounts of pseudoconditioning despite significant differences between animals receiving paired and unpaired training (Abramson & Buckbee, 1995). Pseudoconditioning in proboscis conditioning studies with European bees has been assessed by unpaired and discrimination procedures but was not the subject of investigation in its own right. Pseudoconditioning has been the object of investigation in adult Africanized honey bees and although, the amount of pseudoconditioning observed in those experiments was minimal, it was

argued that some component of acquisition of proboscis conditioning in Africanized honey bees is based on pseudoconditioned responses (Abramson, Aquino, Silva, *et al.*, 1997). The present experiment examined pseudoconditioning in young Africanized honey bees and in adult Uruçu. To our knowledge no studies are reported in the literature that specifically examined pseudoconditioning in young Africanized and stingless honey bees.

Procedure

Eighty, one day old Africanized honey bees were captured from cells, maintained, and harnessed as in the previous series and randomly placed into one of four groups (N = 20). Separate groups of animals received 2, 5, 8, or 11 US presentations before receiving a single CS only test trial. The test trials for each of the 4 groups appeared on trials 3, 6, 9 and 12, respectively. The CS was Africanized honey bee wax, the US a 2 second feeding of sucrose and the intertrial interval 10 minutes.

For the Uruçu experiments, eighty adult animals were captured, maintained, and harnessed as in the previous series. The same experimental design used with day old Africanized bees was adopted with adult Uruçu with the exception of the CS and US. The CS used was the odour of Uruçu wax, the US was a 2 second feeding of Uruçu honey.

The rationale behind selecting beeswax as a CS over the alternatives presented in the first series of experiments is that we wanted to find some effect. For adult Africanized bees, beeswax is potent enough to serve as both a CS and US (Abramson, Aquino, Silva, *et al.*, 1997). We also wanted to take advantage of the fact that beeswax is used in the construction of cells in which the larvae develop and therefore the animals should be familiar with its odour.

RESULTS AND DISCUSSION

Figure 6 shows the mean proportion of one day old AHBs and Uruçu honey bees responding to a single CS only test trial. The figure indicates no pseudoconditioning at any of the 4 test trials.

The low level of pseudoconditioning when beeswax is used is in direct contrast to the results obtained with adult AHBs. In our earlier pseudoconditioning study performed with adults (Abramson, Aquino, Silva, *et al.*, 1997) approximately 50 percent of the subjects (9 of 18 subjects) responded to each of the CS only test trials when beeswax was used.
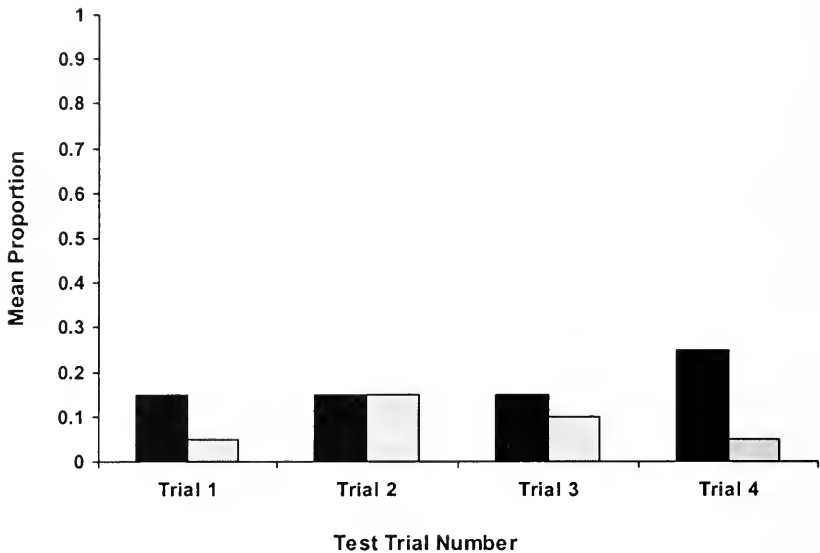
Figure 6. Mean proportion of one day old Africanized honey bees and adult Uruçu honey bees responding to a single CS only test trial. Black histograms represents performance of day old AHBs. Gray histograms represents performance of adult Uruçu bees. No pseudoconditioning is evident.

Results of the ANOVA indicated no Trial effect for the one-day old AHB $F(3, 79) = .768$, $p = .516$, no Trial effect for Uruçu bees $F(3, 79) = 1.034$, $p = .382$, and no Group effect between the AHBs and Uruçu bees $F(3, 152) = .628$, $p = .598$.

SERIES 3: CENTRAL EXCITATORY STATE STUDIES

In the previous two series neither Pavlovian conditioning nor pseudoconditioning was found to occur in day old honey bees or in adult Uruçu. In the present series of experiments the role of central excitatory state was studied. Central excitatory state (CES) refers to the temporary state of "excitement" generated in the nervous system of invertebrates following exposure to a US such as that provided by feeding on sucrose or honey. CES may serve as the basis of pseudoconditioning effects in invertebrates (Terry & Hirsch, 1997).

One hundred and twenty young Africanized honey bees (one day old bees) were selected from the laboratory hives and randomly placed into one of 6 groups consisting of 20 subjects each. They were captured and maintained as in the previous experiments. The primary difference between the groups was the amount of elapsed time between a 2 second

feeding of sucrose and antennae stimulation with spring water. Under normal conditions honey bees will not extend their proboscis to water stimulation. Following a 2 second feeding of sucrose, one group was stimulated three seconds later with spring water, a second group seven seconds later, a third group 15 seconds later, a fourth group 30 seconds later, a fifth group 60 seconds later, and a sixth group 120 seconds later. Stimulation consisted of two strokes of the antennae with spring water saturated filter paper. If the proboscis extended the animal was allowed to feed on spring water for 2 seconds. The filter paper was handled with tweezers.

For the Uruçu experiments, one hundred and twenty adult animals were captured, maintained, and harnessed as in the previous series. The same experimental design used with day old Africanized bees was adopted with adult Uruçu with the exception of the US. The US was a 2 second feeding of Uruçu honey.

RESULTS AND DISCUSSION

In contrast to the Pavlovian and pseudoconditioning findings the results of the central excitatory state experiments are interesting. Figure 7 shows the mean proportion of one day old AHBs and Uruçu honey bees responding at each of the 6 post feeding intervals. Over 70% of the one-day old AHBs in our sample responded to water stimulation following a sucrose feeding at each of the post feeding intervals. Of the experiments reported here this is the first evidence for behavior modification in one day old Africanized honey bees.

The Africanized results are especially intriguing when compared to the Uruçu results. Figure 7 shows that about 50% of the Uruçu bees responded to water stimulation three seconds after a honey feeding. This percentage dropped to 20% seven seconds after the initial feeding. In contrast to the Africanized results no Uruçu bee responded 15, 30, 60, or 120 seconds following the honey feeding.

The results of an ANOVA indicate no Trial effect for the one-day old AHB $F(5, 114) = .348$, $p = .882$ and a Trial effect for the Uruçu bees $F(5, 114) = 13.918$, $p = .000$. A comparison between the one-day old AHBs and Uruçu bees revealed a significant Group effect $F(1,228) = 64.794$, $p = .000$, a significant Trial effect $F(5,228) = 2.296$, $p = .191$, and a significant Group x Trial interaction $F(5, 228) = 2.299$, $p = .046$.
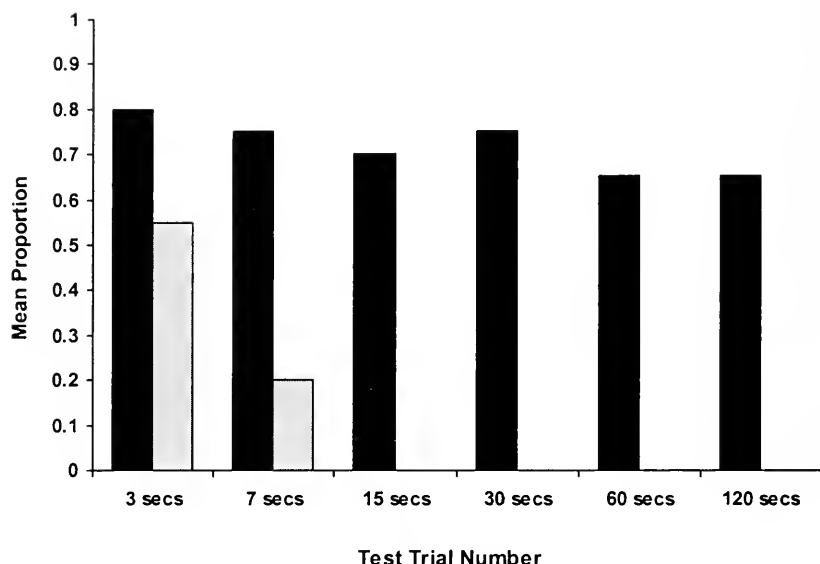
Test Trial Number

Figure 7. Mean proportion of one day old Africanized honey bees and adult Uruçu honey bees responding to water stimulation at each of the six post feeding intervals. Black histograms represents performance of day old AHBs. Gray histograms represents performance of adult Uruçu bees. Central excitatory state is evident in day old AHBs throughout all intervals tested but is restricted to the first interval in Uruçu bees.

SERIES 4: THE USE OF THE PROBOSCIS EXTENSION REFLEX AS A FEEDING ASSAY IN URUÇU

The previous series of experiments suggest that the proboscis extension reflex may not be useful for studies of Pavlovian conditioning, pseudoconditioning nor central excitatory state. The purpose of this series is two-fold. First we wanted to determine if the PER can be used as an assay to develop artificial diets for Uruçu. Second, we wanted to document the inability of sucrose to serve as a US for this honey bee.

Feeding experiments I: Discrimination between sucrose (2.9 M) and dark Melipona honey.

With the exception of one study using softdrinks (Abramson, Aquino, Azeredo *et al.*, 1997) and another using beeswax (Abramson, Aquino, Silva *et al.*, 1997) proboscis conditioning studies use some

type of sucrose solution as a US or reward. In our initial attempts at proboscis conditioning we were surprised to find that sucrose failed to elicit a PER in Uruçu. The purpose of this experiment was to document this failure and to provide evidence that the proboscis extension technique can be used to study feeding preferences in Uruçu.

Twenty subjects were selected from the laboratory colony. Each animal received four exposures to sucrose and honey in a pseudorandom order (ABBA BAAB) where A and B represent the two substances (exposure to the substances were counterbalanced). The duration of feeding time was 2 seconds and there was a 10 minute intertrial interval.

Feeding experiments II: Discrimination between two solutions shown to be effective in Uruçu field experiments.

In attempts to find artificial diets for Uruçu the standard technique is to test the solution under field conditions in which foragers are observed to drink the solution and to return to the hive where the potential food source is placed in honey pots. If the pot is cap the food is considered acceptable to the colony. Such a field test can take two weeks. We believe the proboscis extension technique will provide a more rapid method for testing suitable artificial diets. To examine this idea we used the PER technique to see how readily animals will drink two solutions known to be effective from field studies (Aidar, 1996a, 1996b). One solution is composed of one part water to two parts honey. The other solution is composed of one part water, one part sugar, and one part honey (Alves, 1996). Twenty subjects were selected from the laboratory colony. Each animal received four exposures to both solutions in a pseudorandom order (ABBA BAAB) where A and B represent the two solutions (exposure to the substances were counterbalanced). The duration of feeding time was 2 seconds and there was a 10 minute intertrial interval.

RESULTS AND DISCUSSION

Figure 8a shows the mean proportion of animals feeding on either sucrose or honey (Feeding Experiment 1) and Figure 8b shows the mean proportion of animals feeding on Formula 1 or Formula 2 (Feeding Experiment 2). The two bars of Figure 8a indicate that Uruçu honey bees clearly do not feed on sucrose solutions but will feed on honey. The sucrose results were surprising given how readily *Apis* feeds on sucrose and points to the necessity of having a range of USs available for conditioning studies.
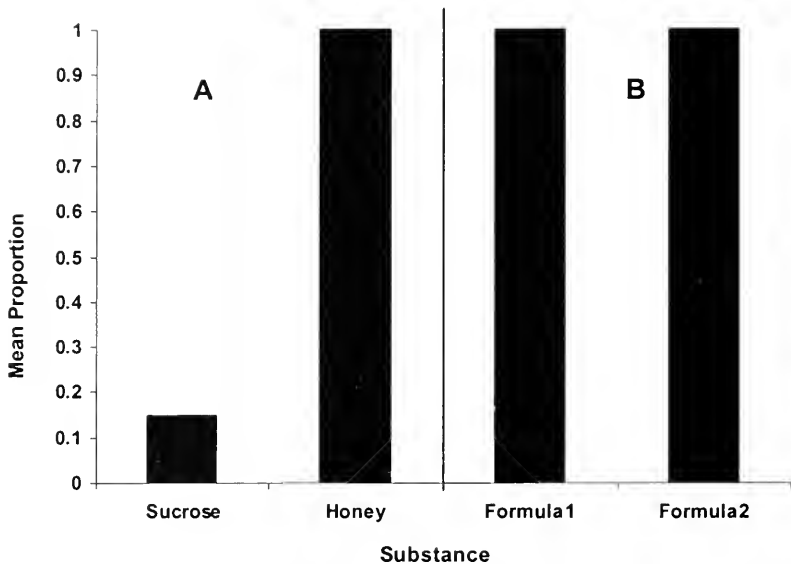
Figure 8. Panel A: Mean proportion of adult Uruçu honey bees responding to sucrose or Uruçu honey in a within subject design. Panel B: Mean proportion of adult Uruçu honey bees responding to two artificial diets in a within subject design. Sucrose is not an effective feeding stimulus for Uruçu bees.

Figure 8b shows that the two artificial diets, shown to be effective in field tests, also elicit feeding in restrained Uruçu. The results of the ANOVA revealed a significant Substance difference between Sucrose and Honey $F(1, 57) = 406.741$, $p = .000$. Because there was no variance between Formula 1 and Formula 2 and between Formula 1, Formula 2, and Honey, no meaningful statistical analysis could be run. It is evident from Figure 8, however, that these substances are readily consumed in contrast to sucrose.

We believe that the proboscis conditioning situation, though not effective in studying conditioning, can be successfully applied as a bioassay to rapidly screen for potential artificial diets suitable for field testing.

GENERAL DISCUSSION

The results of our experiments on the use of the proboscis extension technique to demonstrate learning in one day old Africanized bees and adult Uruçu were disappointing. In the Africanized experiments two different CSs were tried that were known to produce

substantial levels of conditioning in adults (beeswax and Hexanal) as was a qualitatively different CS (water stimulation of the antennae). With all three CSs the performance of paired animals were low (no individual learned) and failed to differ from animals given unpaired CS/US presentations. The Uruçu experiments also employed a wide range of CSs (Hexanal, Geraniol, Citral, Uruçu wax, Africanized honey bee wax, and water stimulation to the antennae) and, as with the Africanized experiments, no conditioning was demonstrated.

The most obvious conclusion from such failures is that the proboscis conditioning technique is not effective with one day old Africanized subjects and adult Uruçu and new procedures need to be developed. There is also the possibility that day old Africanized subjects and adult Uruçu simply do not learn. Bhagavan *et al.* (1994), however, reported that five day old European honey bees could learn a Pavlovian discrimination task - one day old bees were not tested.

Negative results are never appealing and before it can be concluded that day old honey bees and adult Uruçu do indeed fail to learn under proboscis conditioning situations variations in training variables such as intertrial interval, CS and US duration, and stimulus intensity need to be examined. The results of the CES experiment (Series 3) in which day old AHBs responded consistently for two minutes suggests, for example, that lowering the intertrial interval would produce pseudoconditioning.

In addition to the manipulation of training variables we would suggest that training task be manipulated also. It is interesting to note that despite a failure to generate a consistent pattern of conditioned responses, the pattern of unconditioned responses was consistent with previous experiments - all animals responded to the US. The ability to record a consistent US response to sucrose (or honey in the case of Uruçu) suggests that the PER technique may be useful for studies of nonassociative learning such as habituation and sensitization and for associative learning studies involving instrumental conditioning situations such as punishment. The Central Excitatory State experiments clearly show that day old bees are able to modify their behavior. Such behavior is clearly adaptive and has been used to explain some examples of learning in *Drosophila* (Terry & Hirsch, 1997). In contrast to the Africanized experiments, Central Excitatory State in Uruçu was short lived.

The results of the Uruçu feeding experiments were more successful than the conditioning experiments and indicates that the PER technique will be useful in studies of feeding preferences of *Melipona*. As Aidar (1996a, 1996b) and Aidar & Campos (1998) showed, field tests of artificial diets can take two weeks before results are obtained. The PER

method used here is a rapid alternative method of testing artificial diets in which results can be obtained in a single day of experimentation.

ACKNOWLEDGEMENTS

REFERENCES

Abramson, C. I. (1994). *A primer of invertebrate learning: The behavioral perspective.* APA: Washington, D.C.

Abramson, C. I., Aquino, I. S., Silva, M. C., & Price, J. M. (1997). Learning in the Africanized honey bee *Apis mellifera L. Physiology & Behavior, 62*, 657-674.

Abramson, C. I., Aquino, I. S., Azeredo, G. A., Filho, J. R. M., & Price, J. M. (1997). The attraction of Africanized honey bees (*Apis mellifera L.*) to soft drinks and perfumes. *Journal of General Psychology, 124*, 166-181.

Abramson, C. I., Aquino, I. S., & Ramalho, F. S. (1999). The effect of pesticides on the Africanized honey bee (*Apis mellifera L.)* on learning. *Archives of Environmental Contamination and Toxicology, 37*, 529-535.

Abramson, C.I., & Buckbee, D.A. (1995). Pseudoconditioning in earthworms (*Lumbricus terrestris*): Support for nonassociative explanations of classical conditioning phenomena through an olfactory paradigm. *Journal of Comparative Psychology, 109*, 390-397.

Aidar, D. S. (1996a). Multiplição e alimentação artifical de colônias de meliponíneos (Hymenoptera, Apidae, Meliponinae). *XI Congresso Brasileiro de Apicultura*, Teresina, PI, p. 99.

Aidar, D. S. (1996b). A mandaçaia: Biologia de abelhas, manejo e multiplicação artificial de colônias de *Melipona quadrifasciata* Lep. (Hymenoptera, Apidae, Meliponinae). *Sociedade Brasileira de Genetica*, Ribeirão Preto, SP.

Aidar, D. S. & Campos, L. A. O. (1998). Manejo e multiplicação artificial de colônias de *Melipona quadrifasciata* Lep. (Hymenoptera, Apidae, Meliponinae). *Anais da Sociedade Entomológica do Brasil. 27*, 157-159.

Alves, R. M. O. (1996). Meliponicultura: Aspectos práticos. XI Congresso Brasileiro de Apicultura. Teresina, PI, p. 95.

Aquino, I. S., Abramson, C. I., & Payton, M. E. (1999). A rapid bioassay for detection of adulterated beeswax. *Journal of Entomological Science, 34*, 265-272.

Bhagavan, S., Benatar, S., Cobey, S., & Smith, B. H. (1994). Effect of genotype but not of age or caste on olfactory learning performance in the honey bee, *Apis mellifera. Animal Behaviour, 48*, 1357-1369.

Bitterman, M.E, Menzel, R, Fietz, A, & Schäfer, S (1983) Classical conditioning of proboscis extension in honeybees *(Apis mellifera). Journal of Comparative Psychology, 97*, 107-119.

Buckbee, D.A., & Abramson, C.I. (1997). Identification of a new contingency-based response in honey bees (*Apis mellifera*) through revision of the proboscis extension conditioning paradigm. *Journal of Insect Behavior, 10*, 479-491.

Carew, T. J., Marcus, E. A., Nolen, T. G., Rankin, C. H., & Stopfer, M. (1990). The development of learning and memory in Aplysia. In J. L. McGaugh, N. M. Weinberger & G. Lynch (Eds.) *Brain organization and memory: Cells, systems, and circuits* (pp. 27-51). Oxford: Oxford University Press.

Evans, S.M. (1966a). Non-associative avoidance learning in Nereid polychaetes. *Animal Behaviour, 14*, 102-106.

Evans, S.M. (1966b). Non-associative behavioural modifications in the polychaete *Nereis diversicolor. Animal Behaviour, 14*, 107-119.

Getz, W. M., & Smith, K. B. (1987). Olfactory sensitivity and discrimination of mixtures in the honey bee, *Apis mellifera. Journal of Comparative Physiology, 160*, 239-245.

Grether, W. F. (1938). Pseudo-conditioning, without paired stimulation encountered in attempted backward conditioning. *Journal of Comparative Psychology, 25*, 91-96.

Harris, J. D. (1943). Studies of nonassociative factors inherent in conditioning. *Comparative Psychology Monographs, 18* (1, Serial# 93).

Kartzev, V. M. (1996). Local orientation and learning in insects. In C. I. Abramson, Z. P. Shuranova & Y. M. Burmistrov (Eds.) *Russian contributions to invertebrate behavior* (pp. 177-212). Westport, CT: Praeger.

Le Bourg, E. (1996). Hypergravity and aging in *Drosophila melanogaster. Gerontology, 42*, 235-240.

Lorenzon, M. C. (1996). Programa de proteção das abelhas indígenas sem ferrão na Paraiba. *XI Congresso Brasileiro de Apicultura.* Teresina, PI, p. 352.

Mackintosh, N. J. (1974). *The psychology of animal learning.* Academic Press: New York.

Mamood, A. N., & Waller, G. D. (1990). Recovery of learning responses by honeybees following a sublethal exposure to permethrin. *Physiological Entomology, 15*, 55-60.

Menzel, R. (1987). Memory traces in honey bees. In R. Menzel & A. Mercer (Eds.) *Neurobiology and Behavior of Honeybees,* (pp. 310-326). New York: Springer-Verlag.

Menzel, R. & Bitterman M.E. (1983). Learning by honeybees in an unnatural situation. In F. Huber & M. E. Mark (Eds.) *Neuroethology and behavioral Physiology: Roots and Grouping Points* (pp 206-215). Berlin: Springer-Verlag.

Menzel, R, Hammer, M, Braun, G, Mauelshaugen, J, & Sugawa M (1991). Neurobiology of learning and memory in honeybees, in L. J. Goodman & R. C. Fisher (Eds.) *The Behavior of and Physiology of Bees* (pp 323-353). Slough, UK: CAB International.

Mercer, A. (1987). Biogenic amines in the bee brain, in R. Menzel & A. Mercer (Eds.) *Neurobiology and Behavior of Honeybees,* (pp 214-233). Berlin: Spinger-Verlag.

Smith, B.H., Abramson, C.I., & Tobin, T.R. (1991). Conditioned withholding of proboscis extension in honey bees (*Apis mellifera*) during discriminative punishment. *Journal of Comparative Psychology, 105*, 345-356.

Smith, B. H., & Menzel, R. (1989). The use of electromyogram recordings to quantify odourant discrimination in the honey bee, *Apis mellifera. Journal of Insect Physiology, 35*, 369-375.

Stone, J.C., Abramson, C.I., & Price, J.M. (1997). Task dependent effects of dicofol (Kelthane) on learning in the honey bee (*Apis mellifera*). *Bulletin of Environmental Contamination and Toxicology, 58*, 177-183.

Taylor, K. S., Waller, G. D., & Crowder, L. A. (1987). Impairment of a classical conditioning response of the honeybee (*Apis mellifera L*) by sublethal doses of synthetic pyrethroid insecticides. *Apidologie, 18*, 243-252.

Terry, M. G., & Hirsch, J. (1997). The problem of measuring associative learning in *Drosophila melanogaster* with proper procedures to control for nonassociative

effects. In G. Greenberg & E. Tobach (Eds.) *Comparative psychology of invertebrates: The field and laboratory study of insect behavior* (pp. 223-244). Garland Publishing, Inc: New York.

Wells, M. (1968). *Lower animals.* Weidenfeld and Nicolson: London.

Young, J. Z. (1960). Unit processes in the formation of representations in the memory of Octopus. *Proceedings of the Royal Society (Series B), 153,* 1-17.

INTERNATIONAL JOURNAL
OF COMPARATIVE PSYCHOLOGY

INTERNATIONAL JOURNAL
OF COMPARATIVE PSYCHOLOGY

INTERNATIONAL JOURNAL
OF COMPARATIVE PSYCHOLOGY

INTERNATIONAL JOURNAL
OF COMPARATIVE PSYCHOLOGY

Acknowledgement of Reviewers

Instructions to Authors

All manuscripts are reviewed by two readers other than the Editor. Authors should send three copies of their manuscripts to the Editor. One diskette copy saved in ASCII format or as a standard word processor file, will need to be submitted to the Editor once the manuscript is accepted for publication. Electronic versions of figures are also preferred at this stage. Indicate clearly on the diskette the author(s) name(s), file format and program version number. (Alternate arrangements may be possible for those authors who are unable to provide a diskette copy).

The manuscript should have a cover page with the full title, the author(s) name(s) and address(es) and should indicate the person with whom the Journal may correspond. If the author(s) has(ve) an electronic mail address or fax number, these should be given in a cover letter accompanying the manuscript. The abstract should be on a separate page. All articles are published in English; the author(s) should also submit an abstract in their language if it does not require non-Roman type. Author(s) are responsible for the accuracy of the non-English abstract. Acknowledgements should appear on a separate page and carry the title of the article and the author(s) name(s). If the author(s) prefer(s) anonymity in the review process, this should be stated in a covering letter and the manuscript, abstracts, and illustrative material should carry only the title of the article. The cover sheet and acknowledgements will not be sent to the reviewers in this instance.

GENERAL REQUIREMENTS Logical organization is essential. While headings help to structure the content, titles and headings within the manuscript should be as short as possible. Tables and figures should not be redundant. Illustrative material should be self-explanatory and used sparingly. Tables and figures must be in camera-ready condition and include separate captions. Labels on figures should be either Helvetica or Times Roman font and be sufficiently large to allow clarity when reduced. Black and white shading is preferred to more complex fill patterns. Electronic versions of all figures should be included on the final submitted diskette if possible. Only items cited in manuscripts should be listed as references. Page numbers must be provided for direct quotations. Footnotes should not be used except in special circumstances and with permission of the Editor.

MANUSCRIPTS should be double-spaced, the original on white bond paper, with margins of 3 cm on all four edges and approximately 26 lines to the page. Manuscripts longer than 20 typed pages (not counting figures, tables, and references) will only be considered in unusual circumstances. The current style manual of the American Psychological Association is to be followed. Manuscripts which do not meet the style requirements will be returned for retyping.

REFERENCES should be listed on a separate page and referred to in the text by author(s) and year of publication as in the Publication Manual of the American Psychological Association.